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ON THE EYES, THE INTEGUMENTARY SENSE PAPILLÆ, AND THE INTEGUMENT OF THE SAN DIEGO BLIND FISH (TYPHLOGOBIUS CALIFORNIENSIS, STEINDACHNER).

By W. E. Ritter.

With Four Plates.

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No. 3. — *On the Eyes, the Integumentary Sense Papillæ, and the Integument of the San Diego Blind Fish* (*Typhlogobius californiensis*, Steindachner). By W. E. Ritter.[1]

The work the results of which are embodied in the present paper was begun and well advanced at Harvard University, and has been completed at the University of California.

I wish here to express my warmest appreciation of the many kindnesses received at the hands of Prof. E. L. Mark, not only during my residence in Cambridge as a student under him, but particularly since leaving there. I have also to thank Prof. C. H. Eigenmann both for specimens sent me from San Diego while I was working in Cambridge, and for valuable information and suggestions about collecting the fish during my visit to San Diego last summer.

Typhlogobius californiensis was first described by Dr. Franz Steindachner. The species is the type of the genus, and thus far is the only one known. Steindachner's ('79, pp. 142, 143) description of the eyes is as follows: "Die winzig kleinen, wie Punkte durchschimmerenden Augen, liegen hoch am Seitenabfalle des Kopfes gegen Ende des ersten Viertels der Kopflänge; ihre Entfernung von einander steht der Schnauzenlänge nach und beträgt circa $\frac{1}{8}$ der Kopflänge." According to this author the genus resembles Crystallogobius, Gill, from which it differs in its dentition and abortive eyes.

Miss Rosa Smith ('81, pp. 19–21), — now Mrs. C. H. Eigenmann, — unaware that the fish had been described by Steindachner, redescribed it, making for it, as the Vienna ichthyologist had done, a new genus, the name of which was derived from the rudimentary condition of its eyes. *Othonops* was the generic name given it by Miss Smith, and this term, signifying as it does "veiled or obscured eyes," is, so far at least as the younger individuals are concerned, undoubtedly more nearly true to the facts, as the sequel will show, than is the name chosen by Steindachner, *Typhlogobius* signifying "blind goby." The specific name chosen by Miss Smith was *eos*. She says: "This species is most closely related to

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Crystallogobius nilssoni (Düb. & Kor.) Gill (*Gobiosoma nilssoni* Günther, Cat. Fishes Brit. Mus., III. 86), a species found on the coast of Norway, from which it is distinguished generically by the obsolete eyes. . . . The eyes are large and conspicuous in *C. nilssoni*."

With reference to the integument of the head and its tactile organs, this author says: "On the under side of the head the skin (in a preserved specimen) lies in irregular folds, which conform generally to the outlines of the lower jaw, the outer folds reaching the gill openings. Between the lower lip and these folds there is a series of papillæ which has its origin a short distance behind the corner of the mouth, the series being slightly separated close behind the symphysis of the lower jaw by two small, rounded flaps. The papillæ number about fourteen on either side of the flaps. On the superior surface of the snout, extending posteriorly half as far as the termination of the maxillary, the skin is finely wrinkled, and there is on either side a conspicuous flap, which seems to conceal a nostril." The largest specimen examined by Miss Smith was 2¾ inches in length.

The same author ('90, p. 181) publishes a note made by her at San Diego, July 3, 1882, on the tenacity of life exhibited by this species, which is so characteristic of it that I quote the passage nearly entire: "Three specimens were secured and were placed alive in a two-quart tin pail along with seaweeds, polyzoa, hydroids, living mollusks, a sea-cumber, and a number of small fishes and crabs. The living forms in the pail were so crowded and so short of water that all of the fishes except the three pink blind fish had died before I reached home, the drive of twelve miles being over a hilly road for some distance. . . . When returning from La Jolla and other points along the seabeach, I have frequently carried home the tide-pool species alive in this manner, and invariably the Oligocottus analis, one of the small Cottidæ, was more tenacious of life than any of the other species. At this time, however, Oligocottus expired with the rest, leaving the blind fish to claim the honor of being the most hardy of the smaller species of the region. This species is scaleless and exceedingly slippery. I took one of these examples from the pail, when, like an eel, it slipped through my fingers into a barrel of rain water standing near, swimming around in the barrel several times. I then removed it to a clean shallow dish into which I had poured half a cupful of sea sand, together with the small amount of dirty sea water which had covered the medley of animate beings before mentioned. Typhlogobius, still active, tried to bury itself in the sand, but the dish was too shallow, and several efforts proved unavailing. . . .

It was still quite active five hours after it was removed from among the dead fishes. How much longer it may have been able to survive I do not know, as I then killed it with alcohol."

In a paper on the "Point Loma Blind Fish and its Relatives," Prof. C. H. Eigenmann ('90, pp. 65–71) has given some very interesting facts on the habits of the species, and also the only account, so far as I am aware, of some of the profound structural changes that have been induced in it by its peculiar way of living.

The fact that the fishes pass their lives under stones in crab holes, or buried in the sand, must of course have been known by every one who had collected them; but as Prof. Eigenmann has had much better opportunity to study their habits than has any one else who has written on the subject, his account is quite full, and so interesting that I reproduce a considerable portion of it.

About San Diego the fish has been found at Point Loma only; it has been taken, however, at Encenada. Its habitat is consequently, so far as known, quite limited. The crustacean in the holes of which and with which it lives is a burrowing carideoid, which has the same pink color as the fish; but while the crustacean is found throughout the entire bay region, the fish is its companion only at Point Loma. Another species of the Gobiidæ, belonging to the genus Clevelandia, also frequents the holes of the same crustacean along with Typhlogobius.[1]

"Sometimes the fishes [other than the blind fishes?] live quite out of water on the damp gravel and sand under rocks. . . . In the bay the gobies habitually live out of the holes, into which they descend only when they are frightened, while at Point Loma they never leave their subterranean abode, and to this fact we must attribute their present condition."

It is not the eyes alone that have undergone modification. The whole frontal region of the skull has been profoundly changed; the scales have entirely disappeared, the color has been reduced, and the spinous dorsal has been greatly diminished in size. "The skin, and especially that of the head, has become highly sensitized."

[1] I find Clevelandia in San Francisco Bay at West Berkeley; and here it often enters holes in the mud with a species of Crangon. In this case the holes are not, I think, dug by the crustacean. The general appearance and actions of the two animals are so similar that at a little distance it is very easy to mistake the one for the other. The color of the two is absolutely indistinguishable as they rest at the bottom of the shallow tide-pools; and it is so like the dark brown mud of the bottom on which the animals are found that it is with great difficulty that they are seen when not in motion.

In a specimen about 0.9 of an inch long the color cells were well formed, and the membranes of the fins were thin (in the adult the fins are very thick in proportion to their height). The movements of the fish at this age were similar to those of the other gobies, and not at all sluggish, like those of the adult. In the adult, says Eigenmann, "the color has been reduced."

The eyes have suffered the greatest change of all. In the small specimen just mentioned they were quite evident, and apparently functional. "Objects thrust in front of them are always perceived, but the field of vision is quite limited. With age the skin over the eyes thickens, and they are scarcely evident externally. As far as I could determine they do not see at this time, and certainly detect their food chiefly, if not altogether, by the sense of touch."

"The lens is large in proportion to the size of the eye, which does not materially differ in size in the smallest and largest specimens examined. The optic nerve is slender and long as compared with that of any of the other gobies." Because of lack of facilities for histological work, Prof. Eigenmann did not study the minute structure of the eyes. All his attempts to get material for studying the development were unsuccessful, though artificial fertilization was tried, and many visits were made to Point Loma in search of eggs and embryos. The spawning time is June and the latter part of May.

During the last of June and the first of July, 1891, I was able to spend several days at San Diego, but at that time it was impossible to get specimens of the blind fish, a thing which I had greatly hoped to do. From Dr. Eigenmann's experiences I had thought it quite possible that at this time I might also be so fortunate as to get embryonic material of the species. On arriving at San Diego my hopes were at once annihilated, however, as I found that the fish could be caught only at the very low tides, and at this time of the year these tides come in the night. I arranged, however, with two local collectors, Mr. L. C. Bragg and Mr. O. N. Sanford, to have all the specimens they could obtain, as soon as the tides would permit of their being collected, sent to me at Berkeley. By this means I secured twenty-two specimens, the most of them apparently fully grown, though two were considerably smaller than any I had previously studied, and these were all carefully preserved in Perenyi's fluid.

Through the kindness of the officers of the Pacific Coast Steamship Company's steamer "Pomona," twelve specimens were sent to me in July from San Diego alive. Only four of these were living, however,

when they reached me, and only one was in perfect health. This one was kept in an aquarium of about four gallons of water until February 10, 1892. I can fully confirm the statements of other writers concerning the extreme tenacity of life exhibited by these fishes. During the last two months that this specimen was kept, the water was not changed nor aerated in any way, nor was food given to the fish; and I may say that it did not, so far as I could determine, take food at all during the time of its confinement, except the small quantity naturally contained in the water. Worms were placed in the aquarium, but had to be removed, untouched so far as I could see, to prevent contamination of the water by decomposition. When the fish was killed, it was to all appearance as well and as lively as it had been at any time during its captivity.

Experiments for the purpose of determining whether the eyes in this individual still performed their proper function were not very satisfactory. Very frequently when the water was suddenly illuminated by a strong light thrown into the aquarium, standing in a dark room, the fish was found to be moving about at the bottom with considerably more than its wonted activity. This activity would continue for only a short time, when the fish would either move more slowly or would settle down and become quite still. As the movements were almost always rather slow and infrequent when the fish could be seen, I am inclined to interpret this behavior as indicating that the fish was sensitive to the light. However, repeated attempts to produce conditions that would cause it to choose between light and darkness, if it had the power of such choice, were without positive results. On the whole, both from these observations on the living fish, and from the structural conditions to be hereafter described, I am of the opinion that the power of perceiving light is not wholly lost, even in the adult. The specimen kept alive was 32 mm. long, or about 20 mm. shorter than the largest ones that I have seen.

The pink color mentioned by all those who have written of this fish is a quite striking feature in its general appearance. It is not at all due to pigment in the integument, but to the extreme richness of blood-vessels situated in the sub-epidermal connective tissue, as will be shown later. It disappears entirely in preserved specimens, the color becoming a dull opaque white, particularly in large individuals. In small individuals, however, the color of the dorsal side of the head and body is quite dark from the presence of brown pigment. The causes to which these different colors, under different conditions of development and treatment, are due, are of considerable significance, and I shall speak of them more

fully later on. It is not my purpose to give an account of the general structure of the fish in this paper. I must, however, call attention to the far reaching modifications that have been brought about by its peculiar habits, not in the eyes merely, but in many other structures. As already mentioned, Dr. Eigenmann has shown that the "entire frontal region of the skull has been profoundly changed." He has also shown that the fins of the adult are much thicker, more fleshy, and shorter, in proportion to the size of the body, than in the young. My observations fully confirm these statements.

In the smallest specimens that I have seen, 19 mm. long, the eyes are distinctly visible without dissection. In some of the preserved specimens of this and somewhat larger size, the lens is also clearly seen in surface views; while in other specimens it is not so distinct, and in some is scarcely seen at all, though it is probably always present in all these younger individuals.

The eyes are situated wholly on the dorsal aspect of the head, and very near together (Plate I. Figs. 1, 2). Their distance backward from the tip of the nose is also short as compared with the length of the fish. Thus in the specimens 19 mm. long this distance was 0.95 mm., or one twentieth of the entire length of the fish. In large individuals, especially while living, the eyes are visible from the surface, but appear as scarcely more than black specks deeply buried in the tissue. In many cases they cannot be seen at all in preserved specimens.

The epidermis immediately over the eyes does not differ essentially, either in the smaller or the larger individuals, from what will be described further on as existing in other portions of the dorsum and sides of the head and body. The mucous cells are present here as elsewhere, and they are as numerous and as large as in adjacent regions. The average thickness of the epidermis is 50 μ in the smallest specimens studied; 63 μ in a specimen 60 mm. long, and 76 μ in a specimen about 65 mm. long, thus showing a gradual increase in thickness with the increasing size of the animals. In the smallest specimens the sub-epidermal tissue over the eye is not differentiated into a dermal and subdermal layer. The connective tissue in this region is arranged in several strands which unite with one another at various angles, thus bounding wide spaces (Plate III. Fig. 17, *spa.*). In this specimen (Fig. 17) the space between the epidermis and the sub-epidermal tissue is quite wide, and is continuous over the entire eye, and for a considerable distance beyond. This space may be in part artificial; but even if so, the connection between the epidermis and the immediately underlying tissue

must have been exceptionally frail, since separations of this kind are rare in adjacent regions.

The thin layer of tissue next to the lens — in fact closely applied to it in many cases (Figs. 5 and 17, *crn.*) — is part of a layer that envelops the entire eye, in many places lying close upon the pigmented layer of the retina. The portion in the region of the retina is undoubtedly the sclera, and will hereafter be designated as such. The portion in the region of the lens may be regarded as representing all there is of a cornea excepting its epithelial layer; but on this subject I shall speak further presently. The strands of connective tissue that have been spoken of as intervening between the epidermis and the eye in the smaller specimens are distinctly fibrous, and contain numerous small, much flattened connective-tissue nuclei. These strands are directly continuous with the sub-epidermal connective tissue of the surrounding regions, and are not largely continuous with the sclera, though in part they are (Fig. 17 α).

In addition to the small flattened connective-tissue elements in these bands of connective tissue, a few much larger cells are found (*cl. con't.*). They have distinct round nuclei, and each nucleus has a nuclear membrane and a nucleolus. The membraneless cell body is drawn out into one or more processes, usually two or three, which become lost among and are apparently continuous with the fibres of the connective-tissue strands in which the cells are situated. They are probably embryonal connective-tissue cells concerned in the production of the thick layer of this tissue that intervenes between the eye and the epidermis in older specimens (Plate II. Fig. 6). In this older specimen (Fig. 6) a large number of nuclei are seen, in part immediately over the eye, and consequently in the same position as the cells regarded as embryonal connective-tissue cells in the young specimens; but they are mostly at one side of the eye (Fig. 6, *con't. tis.*), and although some of them are undoubtedly cells of connective-tissue character, at the same time many of them are certainly not of this nature, but are probably leucocytes. As shown in Figure 6, there is over the eye in the large specimens a well defined dermal layer, *drm.*, which usually remains adherent to the epidermis when the latter is removed. This layer is nearly structureless, though fine fibres are not uncommon in it. In the specimen shown in Figure 6, the entire thickness of the tissues over the eye is about 392 μ, of which 103 μ is epidermis and 289 μ sub-epidermis. About midway between the epidermis and the eye there is a thin stratum of formed connective tissue (*st. con't.*), much denser than the surrounding tissue; and imme-

diately beneath the dermal layer is a layer of comparatively coarse fibres arranged in bundles running more or less nearly parallel with one another. Among these bundles are blood-vessels and numerous cells, mostly of the kind that I have regarded as leucocytes. The remaining portion of the tissue in this region is composed of rather fine uniform fibres, containing very few cellular elements. I have said that the eye-enveloping portion of the connective-tissue capsule that is immediately over the lens probably represents the cornea, excepting its epithelial layer. When, however, we bear in mind the method of development of the cornea, — as first clearly made out by Kessler ('77, pp. 83–94), and now understood by all embryologists, excepting in so far as this author believed it to contain, besides its epithelial layer, elements derived from the ectoderm; and when we remember, further, that in the cornea of the normal adult eye, the substantia propria, together with the membrana elastica anterior and the membrane of Descemet, make up its entire thickness, excepting its conjunctival (i. e. epithelial) layer, the interesting question arises whether in such an eye as is represented in Figure 6 the layer *crn.* should be regarded as representing the whole cornea, or merely the membrane of Descemet. Should the latter interpretation be adopted, then it would follow that the tissue intervening between this and the dermal layer would be the substantia propria greatly thickened, and the dermal layer (*drm.*) would be the membrana elastica anterior of the cornea; and what I have called embryonal connective-tissue cells (Fig. 17, *cl. con't.*) might then be regarded as corneal corpuscles. However, I hardly think this the right view of the matter, since, as already pointed out, the tissue over the eye is mostly continuous with that of the adjacent regions other than the sclera. It is possible that the strands seen at α, Figure 17, give some support to such an interpretation. But whatever view may be taken, it seems to me that we are justified in regarding the conditions here presented as evidence against Kessler's statement that a portion of the cornea, besides its epithelial layer, is derived from the ectoderm. This author's account of the development of the cornea in Triton is in substance as follows.

The first trace of it to appear is a thin layer of hyaline substance on the inner surface of the ectoderm over the eye. This appears at a time when the cavity of the lens vesicle has wholly disappeared, and the retinal layers have begun to be differentiated. (See the author's Figure 60.) This layer is held to be secreted from the ectoderm. The succeeding steps may best be given in the writer's ('77, pp. 89, 90) own

words: "Wenn die zuerst vorhandene hyaline Schicht eine gewisse Dicke (Figg. 60 und 61) erreicht hat, wird dieselbe vom Hornblatt abgedrängt durch eine zweite an dieses sich anbildende hyaline Schicht; in das zwischen beiden Schichten entstehende Interstitium dringt von der Peripherie her eine einzellige Lage der spindelförmigen Kopfplattenelemente, die sich vorher schon in einen spitzen Winkel gegen das Hornblatt am Rand der Corneaanlage gestellt hatten, ein (Fig. 62); sobald dieselben von allen Seiten her im Pol der Cornea zusammentreffen, ist die erste hyaline Schicht von der unterdess zu der gleichen Dicke entwickelten zweiten vollständig gesondert. Ebenso wie die erste durch die zweite, wird dann die zweite durch eine dritte neu sich bildende Schicht vom Hornblatt und darauf durch eine zweite einwandernde Lage von Kopfplattenelementen von der dritten Schicht isolirt; diese wieder vom Hornblatt durch eine vierte neue Schicht und von letzterer durch eine dritte Zellenlage u. s. f." It would thus appear that a very intimate connection is brought about between the ectoderm itself, the relatively large portion of the substantia propria derived from it, and the mesodermal elements of the cornea; and it should be especially noticed that this process goes on at a comparatively late stage of development, — viz. at a time when the retinal layers are being differentiated, and after the pigmented portions of the eye are well formed; in short, at a stage only a very little earlier than that at which development is arrested in the eye of Typhlogobius. If such a process had ever taken place here, it seems almost certain that we should see some indications of it in such a stage as is shown in Figure 17 (Plate III.). But, on the contrary, what we do find is no connection between the epithelium over the eye and the immediately underlying tissue, or at least almost none, and no indication of a hyaline layer on the inner surface of the epithelium. While, on the other hand, in older specimens (Plate II. Fig. 6) the epidermis and the sub-epidermal tissue are in close connection, there being no interruptions or spaces at all, and we have here a well defined nearly structureless layer closely adherent to the epidermis.

There is considerable individual variation in the size of the eye. In three specimens, 50 mm., 60 mm., and 63 mm. long, the diameters, measured parallel to the long axis of the head, were respectively 0.44 mm., 0.46 mm., and 0.47 mm.; the diameters transverse to the long axis of the head in the last two of these were, respectively, 0.39 mm. and 0.47 mm. In another specimen 63 mm. long, the diameter transverse to the head was 0.372 mm.; the diameter parallel to the long axis of the head was not measured in this specimen. This last measurement was made on the

section, while the measurements in the case of the first three were made with the eyes in place in the head, the head having been cleared in clove oil. It is undoubtedly true, that some of the difference in size between the last mentioned eye and the first three was due to shrinkage in it during its passage through the paraffine. I have made numerous measurements of the same eyes before embedding and after cutting, and have always found the sections somewhat less in diameter than the whole eyes, even when all precautions had been taken to prevent shrinkage. But certainly shrinkage cannot account for the great difference found here between the eye measured in section, and the one of an individual of the same length measured in the head. This small eye, I should add, was the only one that I have found in which the lens was wholly absent. This eye will be described later on. In a specimen 25 mm. long the axial diameter of the eye was 0.28 mm., and its equatorial diameter was 0.45 mm. In a specimen 19 mm. long the diameter in the long axis of the head was 0.28 mm., and transverse to this it was 0.39 mm. It appears from these measurements that the eye does increase somewhat with the increase in size of the animal, though it is true that, in view of the obvious individual variation in size in specimens of nearly the same length, not enough of the smaller specimens have been studied to determine definitely how much this increase amounts to.

A sclerotic coat, well defined from the surrounding connective tissue, is always present, though in some places its fibres, both singly and in bundles, leave their concentric course and pass off into the connective tissue, and thus bring about an intimate connection between the two. In some places the connective-tissue fibres not belonging to the sclera, but in its vicinity, are seen to have taken on a concentric direction even at a considerable distance from the eye, and to have become more numerous and more closely packed than is the case with the subcutaneous connective tissue in general. There is thus brought about a fusion to some extent of the eye bulb with the tissue in which it is embedded. This statement applies especially to the eye the section of which is shown in Figure 6. In most sections numerous flattened connective-tissue cells are found in the sclera ; and in all the eyes that I have sectioned the sclera is cartilaginous in the region corresponding to the ora serrata of the retina. The cartilaginous layer is usually only one cell thick, but occasionally it is two or more cells thick (Figs. 5, 6, and 12). In many specimens the cartilage does not extend entirely around the eye in the equatorial zone, and in no case have I seen it extend more than half-way back to the entrance of the optic nerve. No

indication of ossification of the scleral cartilage, as is common in bony fishes, has been seen. No trace of an argentea is to be found. All the pigment is of the same dark brown granular variety, and, when seen by reflected light, never gives the white, silvery color that is characteristic of the crystalline material of the argentea.

The choroid is exceedingly rudimentary, and in many specimens I have been unable to detect its presence at all. In the eye from which Figure 13 was drawn (Fig. 13, *chr.*), — a specimen the eyes of which, as will be seen further on, are better developed in several respects than is usual in these eyes, — it is more distinctly seen than in any other case that I have studied. Here the layer of pigment is very thin; it is interrupted at short intervals, and cannot be traced for more than one third of the distance through which it would normally extend. Whether this pigment should be regarded as representing the lamina suprachoroidea, or as belonging to the choroid proper, it is impossible to say.

In a few instances (Figs. 13, 14, 15, *chr. cpl.*), a layer of cellular tissue has been found at the proximal pole of the eye, extending for a variable distance toward the anterior rim of the optic cup, but rarely reaching it. This layer is always closely applied to the outer surface of the pigmented layer of the retina, and in some sections it seems to be continuous with the pigment of the choroid. In some places (Fig. 15, *chr. cpl.*) the tissue has very much the nature of formed connective tissue, while in other places (Figs. 13 and 14, *chr. cpl.*) the cells are spherical or elliptical, with indications at times of blunt processes, and with distinct nuclei. Where cells of this kind occur, the layer is somewhat thicker than where the structure is more characteristically that of connective tissue; and in several instances blood corpuscles (Fig. 13, *cp. sng.*) are found scattered here and there in these thicker portions of the layer, indicating the presence of capillaries. I identify this layer as the chorio-capillaris.

A conspicuous structure in all the specimens studied is a thick, usually short, somewhat lenticular mass of pigment occupying a position usually at the proximal pole of the eye, at or near the entrance of the optic nerve, by which it is pierced in some cases (Figs. 14, 15, etc., *gl. chr.*). This mass is concentric with the surface of the retina, but is always separated from it by a short though somewhat variable interval. In some places the cellular layer just described in part occupies this space, and in some places the thin layer of choroid pigment is seen to enter the same space. The mass always lies within the sclerotic, and is always composed entirely of pigment. I have been unable to find any cellular or other protoplasmic elements in it. This body I interpret

as representing the "choroid gland." The evidence for this is principally in the position which it occupies, and very little in its structure. It is true that this body may contain a small amount of pigment in the normal eye, as I find to be the case in Clevelandia, yet its characteristic structure consists, as is well known, in its richness in blood-vessels; but, as already said, none of these occur in Typhlogobius. Its position — viz. at the proximal pole of the eye at or very near the entrance of the optic nerve, and between the chorio-capillaris and the sclerotic — is, however, strong evidence in favor of regarding it as the "choroid gland." This structure is described in text-books (Wiedersheim, '86, p. 412) as being situated in the normal fish eye between the argentea and the pigmented layer of the choroid. The fact that no argentea is present in the eye of Typhlogobius weakens somewhat the force of the evidence that I have used to support the assumption that I have made with reference to the significance of the pigment mass described. But its relation to the chorio-capillaris and the pigment layer of the choroid are the same as that of the "choroid gland"; as is also its relation to the sclera, with the exception that no argentea is interposed between the two. Of course it is impossible to say that, were the argentea developed, it would lie between the sclera and the pigment mass, rather than between the latter and the pigmented layer of the choroid. We however have as much reason to suppose it would occupy the former position as the latter.

The pigment layer of the retina is exceedingly thick. In a specimen about 50 mm. long, the entire thickness of the retina including the pigment layer was 0.108 mm., and that of the pigment layer was 0.07 mm.; while in a specimen of Clevelandia of about the same length, the entire thickness of the retina including the pigment layer being 0.13 mm., the thickness of the pigment layer was only 0.037 mm.; that is, in Typhlogobius the thickness of the whole retina is to the thickness of the pigment layer as 1.5 : 1, while in Clevelandia the corresponding ratio is 3.5 : 1. In Gasterosteus, I find that about the same proportion holds as in Clevelandia, whereas in the perch (H. Müller, '57) the proportion is at least not less, and in the salmon a year old (Hoffmann, '83) the proportion is 6+ : 1.

The layer is composed wholly of pigment of the dark brown granular variety. I have searched in vain for cellular elements within it. In most specimens the pigment is a very uniform mass; but occasionally one finds an eye in which very distinct and perfectly round nodules of pigment occur. Some of these are so clear-cut and smooth in outline that they have the appearance of perfectly round cells wholly trans-

formed into pigment, though they are considerably larger than any cells, even blood corpuscles, that are found in the eye (Plate II. Fig. 13, *glb. pig.*). They probably merely signify that the pigment tends to segregate in such nodules during its formation. On the inner surface processes of pigment project down among the rods, as in normal eyes, excepting that in most instances they are relatively much shorter and less distinct; in some specimens they scarcely appear at all (Plate II., Figs. 5 and 13 *pr'c.*). The greater portion of the thickness of the layer pertains to the region between the bases of these processes, i. e. the terminals of the rods, and the outer surface of the layer. And it is hence in this portion that the increase in thickness over that found in normal eyes has taken place ; for in the latter, this region is relatively thin. I am at a loss to know from what source this pigment has come. As already said, no cellular elements are to be found in the layer, so it is quite certain that they have completely degenerated into pigment. I shall return to this question in the comparative part. The layer thins out rapidly as it approaches the ora serrata, and is frequently thrown into an equatorially directed fold (Plate II. Figs. 5 and 13, *), which may extend entirely around the eye, but more commonly is confined to one side of it.

Immediately in front of the thinned out region just mentioned, the pigment thickens again somewhat, to form the pigmented portion of the iris. This structure, though always present, varies greatly both in form and size. In a majority of specimens the pigmented portion constitutes the entire iris ; and in all cases it forms by far the greater portion of it. The dense pigment is entirely the same in structure as that in the pigment layer of the retina. In the few cases where a cellular portion is present, it is in small quantity, and appears to be of the nature of connective-tissue cells and fibres. Neither blood capillaries nor epithelium have been detected in this region (Figs. 5, 13, and 17, *ir.*). It frequently happens that the outer surface of the iris is in contact with the inner surface of the cornea (see figures), and it is thus made to appear as though the iris has a considerable part in addition to its pigment ; this, however, is undoubtedly only an appearance caused by the inner border of the iris having been thrust outward by some artificial means, — probably by the lens being in most cases moved outward, for this body is very loosely held in its place. In a few specimens a trace of the ligamentum pectinatum is present, though in most cases no trace of it exists. The short blunt processes of pigment occasionally seen projecting toward the lens (Plate III. Fig. 17, β) remind one of the ciliary

processes, but it is extremely doubtful if they should be so interpreted. They are situated too far from the ora serrata and too near the free edge of the iris. They are probably in some way merely incidental to the extensive pigmentation of the iris.

In no instance are the layers of the retina in Typhlogobius as fully differentiated as in the normal eyes of fishes. I will first describe them as they are found in the majority of specimens, beginning with the innermost layer, and will afterwards speak of the cases that show deviations from the common condition.

An internal limiting membrane, distinct from the layer of nerve fibres, I have been unable to find. Corresponding with the exceedingly rudimentary condition of the optic nerve, the layer of nerve fibres is very thin, even in the immediate vicinity of its entrance, where, in the normal retina, it reaches its greatest thickness. In many sections only fragments of it are to be seen; and for considerable areas no traces at all are found. It is possible that its absence is due to its having been broken away during the preparation of the sections; but, however that may be, it is certain that, wherever present, the layer is very thin (Plate II. Fig. 5, Plate III. Figs. 18 and 21, *st. fbr. opt.*). The next layer, viz. that of the ganglion cells (Figs. 18 and 21, *cl. gn.*), is always distinct, and is from one to three or four cells in thickness. As a rule only the nuclei are distinguishable; but occasionally the cell bodies can be made out. Examined under high powers and with careful focusing, some of these are found to possess one or more processes (Fig. 18, *cl. gn.'*). A nuclear membrane can usually be seen, as can also one to several darkly stained particles within the nuclei. The nuclei are in general very nearly spherical, though there is a tendency for them to become elliptical with the longer axis radially directed.

The inner reticular layer (*st. rtl. i.*) is well developed in all cases, and is essentially the same in structure as in the normal eye, though I have not detected any of the fibres running parallel with the surface of the retina that are found in normal fish eyes. Within this layer the radial fibres of Müller (*fbr. Mü.*) can usually be made out, though they appear to be few and indistinct.

The remaining portion of the retina, as far as to the external limiting membrane, is never fully differentiated into the layers that are found in the normal eye between this membrane and the inner reticular layer; and in many specimens scarcely any indication of a differentiation can be seen. About the average condition is shown in Figure 18, *st. rtn.'*, where a layer of nuclei (*st. nl. i.*) about two or three deep may be dis-

tinguished next to the inner reticular layer. These are slightly larger, on the average, than are the more superficially situated nuclei (*st. nl. ex.*), and they also stain somewhat more deeply. Usually each nucleus has a centrally placed nucleolus, and a not very distinct nuclear membrane. These nuclei undoubtedly represent the inner nuclear layer, though whether the entire layer or only its spongioblasts, it is impossible to say.

Following this layer there is usually a single layer of nuclei (*st. rtl. ex.*) that are considerably smaller and less distinct than those of the layer last described. Not only are the nuclei themselves here smaller and less distinct than those of the layers on either side of them, but spaces (*st. rtl. ex.'*) are seen at intervals in which there are no nuclei at all. It seems quite certain that the outer reticular layer is represented by these spaces.

Finally, outside of this layer follows another of nuclei about one or two deep (*st. nl. ex.*) that are again somewhat larger and more distinctly stained than those in the layer last described. No difference between them and those of the inner nuclear layer can be discovered, excepting, as said above, that they are slightly smaller, and stain a little less deeply. They are undoubtedly the nuclei of the rods, i. e. the outer nuclear layer, though I have been unable to trace a connection between them and the rods, and it is somewhat surprising that they are slightly greater in diameter than the rods.

The external limiting membrane (*mb. lim. ex.*) is usually quite distinct.

The rods are well — probably normally — developed, but I have searched in vain for cones. In the retina shown in Figure 18, they are quite variable both in length and diameter, being in a few instances knobbed at the outer ends (*bac. cla.*). It is, however, quite possible that both this appearance and the shortness of some of them are due to artificial causes, but the variation in diameter could scarcely be so explained.

With a single exception, to be described more minutely hereafter, the lens has been present in all the specimens studied in detail.

It differs in no way in structure from the lens in normal fish eyes that I have examined; i. e. it appears entirely homogeneous and structureless after preservation in alcohol, Perenyi's fluid, or picro-nitric acid. It is held in position very loosely, and consequently is easily displaced; it is frequently found, in prepared specimens of the eye, pushed entirely out of its proper situation into the somewhat yielding connective tissue

which lies immediately over it. No trace of a suspensory ligament seems to be present, nor have I been able to find a processus falciformis.

In a single instance, viz. in the eye portions of which are shown in Figures 13 and 21, and which has already been spoken of as showing in several respects a higher state of development than any other specimen studied, I find close behind the iris, within the cavity of the eye, a few strands of tissue containing a few small nuclei, which may possibly be regarded as the hyaloid membrane, though I do not feel at all certain that this is their nature. In the same specimen a very few blood corpuscles are also found close behind the lens within the eye chamber. With this single exception I have been unable to find a trace of tissue within the chamber.

The optic nerve, although exceedingly slender, is always present, so far as my observations have gone. A very striking fact in connection with it is the thick sheath of pigment that surrounds it in its passage through the retina (Figs 6, 13, and 15, *pig.'''*). This sheath invests the nerve very closely, no space existing between it and the latter; however, in its course through the retina, a considerable non-pigmented space is sometimes seen between its outer surface and the pigment of the retina; indeed, in a majority of cases the outer boundary of the sheath can be traced entirely through the retinal pigment.

These facts make me incline to the opinion that this sheath really belongs to the nerve, and has arisen by the pigmentation of the outer portions of it. The fact that in many cases it continues on without interruption through the cellular portion of the retina, nearly to its inner surface (Plate II. Figs. 6 and 13), gives considerable confirmation to this view. It would seem, however, were this the right interpretation, that we should find a rather more gradual disappearance of the pigment in passing, on a section, from the main mass of the wall of the sheath to the unpigmented portion of the nerve, than we do; but the inner surface of the sheath is not quite as sharply defined as its outer surface is.

On account of the position of the eyes, far anterior to the brain, and near the anterior extremity of the head, the optic nerves are very long.

The muscles of the eyeballs (Fig. 8) are also very long and slender, and are probably always present, though I have not been able to detect them in the sections in all cases; but in eyes dissected out and cleared in glycerine or clove oil, or slightly stained in Schneider's acetic acid carmine, I have always found them. Figure 8 is a camera drawing from a glycerine preparation, showing all the muscles excepting the internal oblique, and also the nerve.

I will now describe certain eyes that present exceptions to the conditions already described. The first will be the eye that shows the maximum development; the second, eyes that show the minimum development and the maximum degeneration.

The specimen that shows the greatest development has already been mentioned (page 61) in connection with the choroid and the hyaloid membrane, and the reader is referred to the statements there made concerning these structures.

The most interesting evidence of unusual development is found in the greater differentiation of the layers of the retina; and it is in the greater distinctness of the outer nuclear (*st. nl. ex.*) and outer reticular (*st. rtl. ex.*) layers that the difference chiefly consists (Fig. 21). Whereas the former is ordinarily, as in Figure 18, only one or two cells thick, (exclusive of the cells *st. rtl. ex.*), in this instance it is three or four cells thick; but more significant than its greater thickness is the fact that the deepest cells (*nl. ba.*) are arranged in a regular layer one cell thick, and closely packed.

What this layer of nuclei represents will be pointed out in the comparative part; it may be said here, however, that it probably does *not* belong to tho outer nuclear layer. Although the external reticular layer even here does not present a well defined boundary either internally or externally, — particularly not internally, — the irregular areas which have already been mentioned as being destitute of nuclei in the average specimens (Fig. 18, *st. rtl. ex.'*) are here considerably more distinct (Fig. 21, *st. rtl. ex.*), both as to thickness and frequency of occurrence. In fact, the layer may be regarded as having the characteristic structure of the normal eye, excepting that it contains a considerable number of scattered nuclei, and is without distinct limitation internally. The rods also seem to be better developed in this specimen than in others. In many of them what has the appearance of an indistinct structureless nucleus may be seen occupying the extremity of the fourth of the rod nearest the external limiting membrane (Plate IV. Fig. 22, *a* and *b*). This one fourth probably represents the inner member of the rod. In some cases the nuclear-looking structure terminates on the side directed toward the distal end of the rod with a well defined straight line, but in other cases the whole has a round or elliptical form. This portion of the rod takes stain slightly, but it is the only portion that does. The substance of the remaining portion is uniformly opaque-glassy in appearance, excepting that numerous pellucid spots exist in it. These are considerably more distinct in some rods than in others, and occasionally

they form a regular row through the whole length of the outer member (Fig. 22, *c*). They are mostly confined to the outer members, but in some rods a single one of unusual distinctness is found in the inner member.

I now pass to the least developed and most degenerate eyes. Perhaps the specimen most interesting in this respect is the one shown in Figure 6. In this the lens is entirely absent, a continuation of the pigment layer of the retina extending without break entirely over the space that this structure should occupy. The series of sections of this eye is complete, and every section is as perfect as the one from which Figure 6 was drawn; so there can be no possibility that the absence of the lens is due to artificial causes, or that an error in observation has been made. I should add, also, that I have an equally complete series of sections of the other eye of the same individual, and this shows the same structure in every particular. Over a portion of the outer moiety, the pigment is disposed in a double layer (Fig. 7, *pig.′* and *pig.″*). The outer of these layers is more directly continuous, both in thickness and direction, with the pigment layer of the retina. The inner layer presents a considerably thickened mass, *pig.″*, irregularly lenticular in form. From the appearance shown in this figure, one is tempted to regard this pigment mass as a remnant of the lens, the thinner portion of the layer at its edges, which connects it with the pigment layer of the retina, representing the iris. It is very doubtful, however, if such is the ease. With such an interpretation the outer pigment layer (*pig.′*) would seem to represent the inner layer of the cornea; and this would afford an explanation, not obvious otherwise, of the continuity of the layer over the pupil. But there are several difficulties in the way of these convenient interpretations. In the first place, the pigment mass under consideration is found on examining the entire series of sections to be very irregular in form, and, as shown in Figure 6, to become confluent with the outer pigment layer (*pig.′*) in some portions of the eye; in the second place, as is shown in the figures, and has already been mentioned, the outer layer is directly continuous with the pigment layer of the retina, which of course it should not be if it belongs to the cornea; and, in the third place, the inner layer of the cornea is itself present and not pigmented (Figs. 6 and 7, *crn.*).

Concerning the condition of the retina in this eye I speak with considerable hesitation, because of a fear that its peculiarities may be due to artificial causes. I should say, however, that the specimen was hardened in chromic acid, and that all the tissues around the eye are well

preserved. If the retina is macerated, it is because the preserving fluid failed to penetrate through the pigment layer in which it is wholly incased. Consequently, I shall not dwell at length on the subject, nor insist much on the significance of the structure described. Figure 19 is a rather highly magnified view of a meridional section of the retina near the ora serrata. It will be seen that only the layer of ganglion cells, the inner reticular layer, and undifferentiated layer are here distinguished. The inner reticular layer does not differ from that found in ordinary eyes. But with the other layers the case is quite different. The nuclei are much less closely packed than in other eyes, the intervening spaces being occupied by a few scattered fibres. The nuclei appear to be of two quite distinct kinds. One kind (*leu'cy.*) is somewhat larger than the other, stains considerably less deeply, is less refractive, and shows no trace of a membrane. In the other kind, the nuclei are smaller, *cl.*, *cl.'*, *cl.''*, stain deeply, and are refractive in such a way that in focusing through them they take on the three different appearances shown in the figure; i. e. when seen at a high focus they appear uniformly dark, as at *cl.*; at a deeper focus the appearance is that of a disk with a dark line at its circumference, a light yellow zone (represented in white in the figure) inside of this, and a uniformly dark spot in the centre, *cl.*; at a still deeper focus the appearance is that of a dark ring with a light centre, *cl.''* A few of these latter have two or three longer or shorter processes, but by far the larger number of them are spherical, or nearly so.

No rods are present in these eyes, though this portion of the retina is so ragged and formless that it is impossible to say whether they have ever been developed or not. It is quite possible that the larger bodies, in which, however, no nuclei are visible, are leucocytes.

Another interesting exceptional case is that presented by the section of the eye shown in Figure 12. It will at once be seen that the point of chief interest lies in the double layer of pigment that is situated behind the lens within the cavity of the eye. The outermost of these layers is in close contact with the posterior surface of the lens, while the innermost is in close contact with the inner surface of the retina. I cannot, however, satisfy myself that either layer is developed at the expense of the parts to which they are respectively adjacent. It is true that the line of contact between the lens and its pigment layer is not a sharp one, there evidently being a gradual disappearance of the pigment here. The lens, however, shows no flattening on this side, as it would were the pigment layer formed at its expense; but more than this, the

pigment layer extends on either side beyond the lens, its outer edge becoming on one side (the lower one in the figure) continuous with the inner layer of pigment, and on the other side with the pigment layer of the retina. The connection with the outer is shown rather indistinctly in the section figured, but much more distinctly in some of the other sections of the series, as is also the fact that at places the iris is entirely cut off from the retinal pigment. If, then, these layers of pigment have come neither from the lens nor the retina, the only other structures in this region that they could come from are the vitreous body and the hyaloid membrane. In other respects this eye does not differ appreciably from the usual structure already described, with this exception, that the undifferentiated layer of the retina shows somewhat less differentiation than usual. I have studied these sections in vain to find convincing evidence of actual degeneration within the retinal elements themselves, in addition to the pigmentation.

I now present a table showing some of the results of measurements that have been made of the retina, lens, and optic nerve : —

	Two Specimens, each 19mm. long.		Spec. 50mm. long.	Spec. 60mm. long.[1]	Spec. of Clevelandia.
	1	2	3	4	5
	mm.	mm.	mm.	mm.	mm.
Entire retina (including pigment layer) . . .	.095	.075	.110	.145	.136
Pigment layer	.055	.046	.063	.078	.042
Nerve fibre layer	.0029	.0014	.0043	.0058	.05
Ganglion cell layer	.004	.0029	.0072	.0058	.05
Inner reticular layer	.013	.0058	.0116	.018	.021
Undifferentiated layer	.017	.001	.0203	.0317	
" Undifferentiated layer " of Nos. 1, 2, and 3:					
Outer nuclear layer				.0058	.016
Basal nuclei in outer nuclear layer . . .				.0029	.0029
Inner nuclear layer (including outer reticular layer)				.0023	
Outer reticular layer					.0018
Tangential cell layer					.0029
Inner nuclear layer					.029
Diameter of lens		.205			.784
Thickness of optic nerve at entrance to retina				.011	.117
Length of rods				.032	

Perhaps the most important thing that these measurements reveal is the fact that the eyes are subject to great variation, as well in the pro-

[1] The same specimen from which Figures 13 and 21 were drawn.

portion of their constituent parts as in their size and degree of differentiation in different individuals.

It is quite probable that some of the differences in thickness between the retinas of different individuals is due to the fact that measurements have been made on sections not quite meridional in direction. Care has been taken, however, in each instance to avoid this source of error. But in the case of the one giving a thickness 0.145 mm. greater than that of the normal retina in Clevelandia, the sections are so cut that none are quite meridional. As may be gathered from Figure 13, this eye is so flattened in its axial direction that the retina is almost disk-shaped; and from this fact it was possible so to cut the retina that none of the sections would be entirely perpendicular to its surface. The sections *are* so cut obliquely, though the deviation from the perpendicular is certainly not sufficient to account for the great difference in thickness that is shown. But the difference in proportion between corresponding layers in different retinas cannot be explained, even in part, as due to artificial causes. In one of the specimens 19 mm. long, the ratio between the inner reticular layer and the whole retina is 1 : 7, while in the other it is 1 : 13.

From the measurements here given alone, it might be concluded that there is a gradual increase in thickness, and a constantly advancing differentiation in the retina, with increase in the size and age of the animals. Such a conclusion is not warranted, however, when the whole number of specimens and stages that have been studied by me is considered, though it must be admitted that, in view of the obviously wide range of individual variation, the number of specimens examined has not been sufficiently large to justify an unqualified denial that such is the case. All that can be said with positiveness is, that, notwithstanding the fact that the thickest and most fully differentiated retina has been found in a specimen much larger — and therefore presumably older — than the smallest studied, yet several still larger individuals have shown retinas thinner and less differentiated than those of the smallest individuals; and, further, that in one instance at least one of the smallest individuals shows in the distinctness of the outer reticular layer as great a degree of differentiation as any retina examined. It would be a very interesting and significant thing, if, owing to a retardation in development, differentiation of the retina should continue throughout the entire life of these fishes; since we know quite well that normally the fish eye becomes functional and differentiated at an early period in development (Balfour and Parker, '82, pp. 371 and 384; Ryder, '84, p. 500; Hoffmann, '83).

It is exceedingly desirable to ascertain what law, if any, controls the

variations of functionless organs. Having now before us the facts relating to the structure of the eye, we may pass to some reflections on their significance when considered from a comparative and a developmental point of view.

First of all, I will speak of the pigment layer of the retina. This has the greater interest since, according to R. Wright (Wiedersheim, '86, p. 427), in the retina of the "blind fish Chologaster papilliferus there is no pigmented epithelium."

It has already been shown that in Typhlogobius this layer is always thicker, relatively, than in the normal fish eye, being thicker than the entire remaining portion of the retina. I am in considerable doubt as to how this thickenning has taken place. The first explanation that suggested itself to me was that the choroid had become wholly converted into pigment and fused with the pigment lamella of the retina. However, the dense and uninterrupted character of the pigment of the layer, and the evenness of its external surface, at once threw grave doubts in the way of this explanation, and the more because of the rather meagre development of the choroid in the normal eye of bony fishes. Then, as the choroid was found on further study to be present outside of this layer, the only remaining alternative was to suppose the latter to be wholly derived from the proximal wall of the primitive optic vesicle; i. e. to represent the pigment lamella of the retina. We may possibly suppose that the proximal wall of the primitive optic vesicle never became thinned out as it does in normally developing eyes; but the fact that this process takes place very early — in bony fishes, at least, by the time the differentiation of the retina has begun — is quite a serious objection to such a supposition. But even if this were the case, it is hardly possible to believe that this layer was ever as thick as we find the pigment layer in the adult fish to be. We seem forced to suppose that for some reason the layer has actually increased in thickness concomitantly with the retardation in the development of the eye, or, it is quite possible, with the *degeneration* of this particular part of it.

I would call attention to the comparison of Typhlogobius with Clevelandia in this regard. From the figure of the retina of the latter, it will be seen that the retinal pigment appears in two quite well marked layers, an outer and an inner, the two being connected at short but somewhat irregular intervals by crossbeams or processes (Fig. 20, *ex.*, *i.*, and *m.*). From this it seems that the inner extremities of the processes of the retinal pigment layer, which in normal eyes, and particularly in many teleostean eyes, project far down among the rods and

cones, have here become fused together to form a continuous inner layer, *i.*

So far as I have been able to determine, this condition is peculiar to Clevelandia, at least to the extent in which it is here seen. The interesting question now arises whether we have here the beginning of a process that would, under conditions that have brought about the changes seen in the Typhlogobius retina, ultimately result in a similar thick, solid retinal pigment layer; this being effected by a still further fusion of the cross rods of pigment now seen. As already pointed out, it is certain, both from Dr. Eigenmann's observations and my own, that Clevelandia spends some time at least in holes in the ground.[1]

The only doubt existing concerning the identification of the layers of the retina is with reference to what I have called the outer reticular layer (Plate III. Figs. 18 and 21, *st. rtl. ex.*), and the layer of nuclei (Fig. 21, *nl. ba.*) that has been designated by the non-committal term of "basal nuclei," *basal,* i. e., with reference to the outer nuclear layer. On comparing Figure 21 with Figure 20, the section of a Clevelandia retina, there will be little doubt of the correspondence of layer *nl. ba.* in the two cases; but at the same time the entire absence of layer *ful.* (Fig. 20) will be noticed in Figure 21. These two layers together seem to correspond to W. Müller's ('74, pp. 60 and 61, Taf. XIII. Figs. 4 and 7) layer of tangential fulcrum cells. This layer is described by this author as being composed in Petromyzon of "zwei Etagen grosser quadratischer Zellen, zwischen welchen eine Schicht ganz flacher, in faserartige Ausläufer sich fortsetzender Zellen gelagert ist." The layer is said, in the same connection, to be subject to much modification in the different families of fishes, in which alone it is well developed; but the Percidæ and the Cyprinidæ are mentioned as teleostean groups in which the layer with both its "Etagen" is present. According to this interpretation the external granular layer of M. Schultze, called in this paper the external reticular layer and by Krause ('76) the membrana fenestrata, is not present in either Clevelandia or Typhlogobius; and it is instructive to note that Krause does not find this

[1] I may here add an observation recently made, which indicates that the time thus passed hidden from the light is not inconsiderable. On some of my visits to the beach at West Berkeley I have found the fish very numerous in the tide-pools, while at other times hardly any are seen. Whether their absence is due entirely to their having gone into the holes I am not sure; but however that may be, at such times I have occasionally found them by digging. I am not yet able to say whether their disappearance is in any way correlated with conditions of the weather as regards sunshine.

layer in Perca fluviatilis. Its position would be between the external nuclear layer and the layer *nl. ba.* (Figs. 20 and 21). The outer of the two "Etagen" of Müller's tangential fulcrum cells appears to correspond to Krause's membrana perforata, and likewise to M. Schultze's basal plexus, and the inner to Krause's stratum lacunosum; this would make the layers *nl. ba.* and *st. rtl. ex.* of the Typhlogobius retina the membrana perforata and the stratum lacunosum, respectively. An objection to this interpretation is possibly presented by Hoffmann's account of the development of the Salmon retina. His Figures 10, 11, and 12 (Taf. V.) show that what he calls the tangential fulcrum cells become differentiated quite early, certainly as early as the stage of development represented by the partially developed retina of the adult Typhlogobius. But judging from the position of this layer in relation to the inner nuclear layer and the layer that he regards as the outer granular layer, it would seem that his tangential fulcrum cells correspond to the inner "Etagen" only of what Müller designates by that name. But according to my interpretation these cells are not present in Typhlogobius, unless they be represented by the scattered cells in layer *st. rtl. ex.* The chief point to be made in this discussion of the homologies of the retinal layers is this. In the most differentiated retina, even though all the layers found in the normal adult fish eye may be marked out, the differentiation is much less complete as regards the zone between the two nuclear layers than it is in the normal eye of a closely related genus; while in a majority of individuals development is arrested at a considerably earlier stage.

In view of the almost universal statement that the rods and cones are the latest of all the parts of the retina to be developed, it would, I think, hardly be expected that the rods should be as complete as they are in these eyes. O. Hertwig ('90, p. 402) says, "Of all parts of the retina the remarkable rods and cones are the latest developed." Hoffmann ('83, p. 68) says, "According to all other authors [Löwe excepted] they [the external members of the rods and cones] arise latest of all the retinal elements in the different animals; and it is likewise so in bony fishes." It would certainly seem that the testimony of the eyes of Typhlogobius is against the absolute correctness of these statements.

The recent papers of Hess ('89), Kohl ('89), and Schlampp ('91 and '92) together with the somewhat older contributions to the same subject by Leydig, Kadyi, Ciaccio, and others, make possible a detailed comparison of the eyes of Typhlogobius with those of Proteus anguineus and Talpa europea.

On the whole, it appears that the eye of Proteus is more rudimentary than that of either Typhlogobius or Talpa. The most distinct indication of this is in the absence of the lens in the adult animal.

With reference to it Schlampp says ('92, p. 555): "Die Linse [in Proteus] wird gleichzeitig mit der Einstülpung der primären Augenblase angelegt, wächst in den sekundären Augenbecher hinein, wo sie bei der Larve noch in der Gegend des vorderen Augenpoles zu finden ist. Sie kommt aber über die zellige Struktur der embryonalen Linse nicht hinaus, erleidet vielmehr durch Nichtgebrauch alsbald eine Rückbildung, so dass sie bei ganz jungen Thieren an Grösse und Zellmasse schon bedeutend reducirt ist, im späteren Leben aber resorbirt wird und spurlos verschwindet."

The lens is present in Talpa, though it retains its embryonic cellular structure throughout life, wholly according to Hess ('89, p. 8), partly at least according to Kohl ('89, p. 385) and others. In this regard, then, it is more rudimentary than the lens of Typhlogobius. The choroid is present in Proteus, consisting, according to Kohl ('89, p. 406) "aus mehreren Zellenlagen mit reichlichem Pigment, das sich stets in zwei Lagen anordnet, von denen bald die eine, bald die andere die grössere Stärke besitzt. Die innere derselben repräsentirt das vielfach (so auch Hess) schon zur Retina gerechnete Pigmentepithel." It also contains blood capillaries according to both Kohl and Hess. As regards the choroid and the pigment lamella of the retina, it would seem, according to these statements, that the eye of Typhlogobius, with its exceedingly rudimentary choroid and greatly thickened pigment lamella, is somewhat more rudimentary — it may be even degenerate — than that of Proteus; though it must be borne in mind that the choroid is comparatively feebly developed in normal teleostean eyes.

In Talpa the choroid reaches a relatively slight development, and has little pigment, while the pigment layer of the retina is highly developed (Hess, '89, pp. 3 and 4). In this regard it more nearly agrees with Typhlogobius than does Proteus. The iris, considerably thickened with pigment, the ligamentum pectinatum, ciliary body, and ciliary muscle, are all present, though reduced, in Talpa, according to Hess.

With regard to the retina of Proteus, Schlampp's statement in his summary is as follows: "Die Retina breitet sich, Mangels des central Glaskörperraumes, nicht flächenhaft aus, sondern wird eine solide Kugel, welche axial von Sehnerven durchzogen wird. In ihrem histologischen Baue weicht sie nicht wesentlich von der Netzhaut der Amphibien ab, die Endapparate erreichen aber die endgültige Form nicht."

Also according to Kohl ('89, p. 407), the nerve-fibre layer, the ganglion-cell layer, the inner and outer nuclear layers, and the inner reticular layer are present. Regarding the outer reticular layer and the optic cells he says: "Zwischen den beiden Körnerschichten habe ich die aüssere reticuläre Schicht (Zwischenkörnerschicht) immer durch eine fortlaufende, oft gar nicht so schmale Spalte repräsentirt gefunden. . . . Die Sehzellen, die sich mit Picrocarmin meist sehr schön färben lassen, zeigen ungemein mannigfache Formen: bald ganz flach, bald nahezu kreisrund. Oefter fand ich vollkommen entwickelte Zäpfchen, niemals jedoch auch nur annährend stäbchenartige Gebilde. Die Hemmung in der Entwicklung ist eben auch hier schon so früh eingetreten, dass eine ausgesprochene Stäbchen- und Zapfenschicht nicht mehr zur Ausbildung kommen konnte."

Of the retina in Talpa, Hess says that the nerve-fibre layer is very thick near the entrance of the optic nerve, and that the inner reticular layer contains cells; he quotes Leydig and Kadyi to the effect that the optic cells consist exclusively of rods, and he adds ('89, p. 5), "Ueber die anderen Retinaschichten ist Besonderes nicht hervorzuheben." Kohl ('89, p. 384), however, states that "Zäpfchen sind stets vorhanden: oft vereinzelt, oft sehr zahlreich und die Stäbchen nahezu verdrängend. Bei einem Exemplar zeigen die Sehzellen noch jene Form, die sich bei Embryonen eines gewissen Alters findet, und noch nicht erkennen lässt, ob die betreffenden Zellen sich zu Stäbchen oder zu Zäpchen weiter entwickeln werden." It thus appears that the three retinas have reached about the same stage in development; that of Proteus being probably on the whole the most rudimentary, and that of Typhlogobius, at any rate as represented by the one shown in Figure 21, the least so.

As regards the vitreous body, Schlampp finds that it is entirely absent in the eye of Proteus; while Kohl ('89, pp. 406 and 407) finds a structure which he regards as the hyaloid membrane, or "the membrana limitans interna, the only representative of the vitreous body in the Proteus eye." Hess and Kohl both describe the vitreous body as present in Talpa, and, according to the latter, it contains numerous blood-vessels. It will be remembered that no trace of this structure has been found in the eye of Typhlogobius, with possibly a single exception.

All are agreed at present, it appears, that the optic nerve is present in both Proteus and Talpa, though Hess quotes Semper as stating that it is entirely degenerated in Talpa. I find no account, however, of its ever having in either of these animals a pigment sheath in its passage through

the retina, such as occurs in Typhlogobius. But it is interesting to notice in this connection Kohl's description of this portion of the nerve in Proteus. He ('89, p. 408) writes: "Beim Durchgang des Opticus zeigen die Zellen der Retina ein eigenthümliches Verhalten. Ihre Kerne werden sehr langgestreckt und sie ordnen sich um den Nerv in 1-2 dichten Lagen dergestalt an, dass sie schon kurz vor dem Eintritt des Opticus in die aüssere Körnerschicht und auf der ganzen Strecke, die derselbe sich durch die Körnerschichten hinzieht, eine Art fester Röhre um ihre bilden." It is quite possible that the pigment sheath described in the Typhlogobius eye may have been preceded by such a cellular sheath as this; but if so, my conjecture that it is derived from the nerve itself, and not from the surrounding retina, would be, of course, erroneous. It is also worth mentioning that Berger ('81, p. 262) has described pigmented fibres arising from the choroid as passing through the optic nerve in some fishes.

We have not yet sufficient knowledge of the minute structure of the eye of any of the other blind vertebrates, Myxine and its allies excepted, to make possible further detailed comparison. With reference to the eyes of the Myxinidæ, it should be said that, from the investigations of J. Müller ('35–41), and, later, W. Müller ('74, pp. 7–15), we know that they are far more rudimentary than in any other vertebrate whatever, unless we admit the exceedingly problematical pigment spot at the anterior end of the nerve cord of Amphioxus to be homologous with the eye. It is, however, instructive to notice wherein the eyes that we have been considering may be regarded as passing along the same degenerative road over which the Myxinoid eye has passed, and in what respects they might seem to be on different roads. The eye of Myxine is buried in the tissue of the head in much the same way as in the other forms, excepting that, in addition to the layers of skin and the connective tissue by which it is covered, there is also a layer of muscle over it, and it is immediately surrounded by a sort of capsule containing in its substance much fat. As the foregoing pages have shown, there is no indication of either the muscle layer over the eye or the fatty layer around it in Typhlogobius, Proteus, or Talpa; but it is of course entirely beyond our power to say that there never could be such structures.

Neither lens nor eye muscles, nor anything that can properly be regarded as a cornea, sclerotic, or iris, are present in the eye of Myxine. The primitive optic vesicle never becomes wholly obliterated, and the retina reaches only a very rudimentary degree of differentiation. W. Müller ('74, p. 14, and Fig. 3, Taf. XI.) recognizes in it, however, the

internal limiting membrane; the inner reticular layer (called by him the neurospongium), and scattered in this the ganglion cells; the inner nuclear layer (called by him the ganglion retinæ); the rudiments of the rods and cones; and the radial fibres. Krause's remarks on the eye of Myxine are interesting. He ('86, p. 19) says: "Sein Auge würde zu den *perotischen* rückgebildeten, wie das von Proteus anguineus zu rechnen sein, und man kann die rudimentär entwickelte Retina deshalb nicht zur Construction phylogenetisches Aufbauten benutzen." It appears to me that the most interesting fact concerning the Myxinoid eye, at least from a comparative point of view, is the entire absence of pigment in it. I may here say that I have made some sections of the eye of a member of this family found at Monterey, Cal., and named by Lockington ('78, p. 793) Bdellostoma stoutii, and can confirm the statements made on this point by all other observers. I have so far found no trace of pigment in the eye. The proximal layer of the primitive optic vesicle remains distinctly cellular throughout life, as always stated, but no pigment appears either in it or in the mesodermal tissue immediately surrounding the eye. If, as seems certain with the rudimentary eyes of the three forms that we have been considering, an increase of pigment is an incident to the gradual diminution in functional importance and structural completeness, I can see no very satisfactory explanation for the absence of pigment in the Myxinoid eye, if we are to suppose, as I take it for granted we must, that it too is the result of arrested development.

Wyman ('54, p. 395; '54[a], p. 18; see also Putnam, '72, pp. 18, 19) has made us acquainted with the eye of Amblyopsis spelæus as far as he was able to with the methods of morphological investigation of his time. And it is altogether probable that all he has made known concerning this species holds good for Typhlichthys subterraneus, since the two forms are so nearly alike that systematists are not fully agreed that they should be considered as separate species.

According to Wyman, the eye of Amblyopsis has "a sclerotic coat, a choroid coat, a layer resembling the retina, a lens, and a nerve." His notes, published by Professor Putnam, give somewhat more of detail as to the structure of these several parts. He says: "Under the microscope, with a power of about twenty diameters, the following parts are satisfactorily made out: . . . 2d, a layer of pigment cells for the most part of a hexagonal form, and which were most abundant about the anterior part of the eye; 3d, beneath the pigment a single layer of colorless cells, larger than a pigment cell, and each cell having a

distinct nucleus; 4th, just in front of the globe a lenticular-shaped, transparent body, which consisted of an external membrane containing numerous cells with nuclei." The pigment layer he regards as representing the choroid, and the layer of colorless cells within — and it should be particularly noticed that it is according to both his description and figures a *single* layer — as representing the retina. It is very desirable, indeed, that these eyes should be studied anew with modern methods of preservation and by means of sections; for, if Wyman's account of the structure proves to be correct, we have here a most interesting deviation from the three forms best known and already compared. It may be supposed that his statement concerning the cellular condition of the lens is correct; for this involves merely the observation that a given structure is composed of cells, while his statement concerning the retina involves an observation as to how the cells in a given cellular structure are disposed, — two quite different matters, as every histologist knows. In this particular the lens of Amblyopsis corresponds, then, to that of Talpa; but in the latter animal the retina is fairly well differentiated, and even in Proteus, where the lens is wholly wanting in the adult, the retina is differentiated to a considerable extent. If Wyman is correct in supposing that the retina in Amblyopsis is represented by a single layer of cells, then we have a condition corresponding more nearly to that found in Myxine than in any other known vertebrate, although even here the retina proper is far from being a single cell layer, but the eye of this latter form has no trace of a lens.

Cope ('64, p. 232) remarks with regard to the blind Silurid, Gronias nigrilabris, that in no case has he found anything representing the lens. Whether a considerable number of specimens were examined with reference to this point, the author does not state; but from the general character of the fish and its eyes, as described, it appears to me quite probable that, as Packard suggests, further examination will lead to the discovery that the lens is not entirely absent.

I cannot refrain from saying at this point a few words on the question which, in reality, induced me to undertake the study of the eye of Typhlogobius, viz. the question of the actual degeneration of functionless organs. There is a belief prevalent among zoölogists, though to just what extent I am unable to say, that, if a structure undergoes degeneration in ontogeny it does so in the reverse order of its phylogeny. It would appear that a degenerating vertebrate eye with its great complexity of organization, this complexity having been taken on by degrees

through a long course of evolution, would furnish an excellent test of this belief. The eye here studied throws very little light on the question, however, — scarcely as much as does that of other known functionless eyes. But when we consider together the facts presented by the eyes of Myxine, Typhlogobius, Proteus, and Talpa, and possibly also Amblyopsis and Gronias, this much seems quite certain: that the lens disappears before the retina; and that, where degeneration takes place at all in ontogeny, the lens is affected first and most profoundly, as seen in Proteus, and probably also exceptionally in Typhlogobius. Supposing the somewhat doubtful instance of a degenerating retina presented by the eye shown in Figure 19 to be genuine, we still have reason to believe that its degeneration has been preceded by that of the lens, since the latter body is undoubtedly absent in this specimen. There can scarcely be a doubt, from physiological reasons, that the retina is considerably older, phylogenetically, than the lens, even though it can hardly be said to be so ontogenetically.

The Integumentary Sense Organs.

At present I treat this subject no further than pertains to the question whether the loss of sight in Typhlogobius has been compensated by an unusual development of the sense of touch, leaving the consideration of any morphological significance that the sense papillæ may have with the hope that they may be studied developmentally at some future time.

From the testimony of numerous writers, there is no doubt that compensations for such loss by the super-development of the other special senses, hearing, smell, and touch, are common among animals both invertebrate and vertebrate. For a discussion of this subject see Packard ('86, pp. 123–130).

My conclusion with reference to the tactile sense in Typhlogobius is, that in all probability it not only has not increased, but has actually diminished *pari passu* with the diminution of the power of sight. The reasons for this conclusion are that several — at least four — genera of the Gobiidæ closely related to Typhlogobius are as well provided with tactile papillæ as is the blind fish, these organs being considerably more numerous and more widely distributed on different parts of the body in the other fishes than in Typhlogobius. The genera to which I refer are Gobius, Gobiodon, Lepidogobius, and Clevelandia. The last two I have examined myself. The arrangement and

distribution of the papillæ of Typhlogobius are shown, except for a few scattering ones to be spoken of shortly, in Plate I. Figure 3, *pap.*

There are two series near the edge of each side of the lower jaw, running parallel with it. The series of one side do not quite unite, anteriorly, with those of the opposite side, the interval between their ends being occupied by a slight prominence in the epidermis. Posteriorly the series extend beyond the angle of the mouth and turn upward somewhat to terminate about on a level with the mouth opening; the rows nearer the median line, however, extending slightly farther than the ones nearer the edges of the jaws (Fig. 3). The papillæ of the inner series are considerably larger than those of the outer series, there being about six of the former to thirteen of the latter. The larger ones are on the average about 0.08 mm. in diameter, though the size varies considerably. The papillæ of the outer series are situated on a quite prominent ridge, while the inner ones are, on the contrary, in a shallow furrow. These ridges and furrows are, however, apparently a part of the longitudinal foldings in the integument that are characteristic of this region of the head, rather than structures expressly for the accommodation of the sense buds. Another series of papillæ is found on each side of the head above the mouth, and having very nearly the same direction as those below, though inclining toward the latter somewhat in their course backward. These extend anteriorly to near the tips of the fleshy knobs shown at †, Figure 1. The papillæ above the mouth are of about the same size as the smaller ones on the lower jaw. Still another series is found on each side of the head on the operculum, extending however at a right angle, or nearly so, to the series already described (Fig. 3). These are also of the smaller variety. The number in both this and the upper-jaw series is more variable that in the lower-jaw series, though the transverse series never extend far on to the top of the head.

In Lepidogobius and Clevelandia both lower-jaw series are present, and have precisely the same arrangement and form as in Typhlogobius; and in addition papillæ are numerously present on various parts of the head and body where they do not occur in Typhlogobius. Thus on the head of Lepidogobius there are at least several hundred in addition to the ones on the lower jaw. On each side of the head, beginning at a point a little above the mouth and somewhat nearer its angle than the end of the snout, four rows take their origin and diverge irregularly. The row nearest the mouth bends downward somewhat as, in its backward course, it reaches the angle of the mouth, and it extends,

as do all the rows, considerably farther back of the angle of the mouth than it does in front of that point. The uppermost row of the four runs upward to near the posterior and lower quadrant of the eye, where it takes a trend more directly backward, and extends for a considerable distance back along the dorsal limit of the operculum. The other two rows are situated considerably nearer the lower than the upper row, and are nearer each other than either is to the uppermost or the lowermost row. They also run very nearly parallel with each other. The lower one of these two middle rows contains the fewest and largest papillæ of the head, those of the inner mandibular series excepted. There are about twenty-five papillæ in the lower row, nineteen in the next, thirty-five in the third, and fourteen in the fourth.

Head of Lepidogobius, showing the distribution of the tactile Papillæ. × 1½.

Many of the papillæ of this species are distinctly excavated on their summits, and in such a way as to show such an arrangement as is described by Solger ('80, p. 375) to exist in the lower jaw of Gobius minutus. The excavations are in the form of grooves, or creases, which extend entirely across the summit of each papilla, each groove being somewhat broader in its middle than at the ends. In some of the rows these grooves are directed lengthwise of the row, while in others they have a direction crosswise of it. There is some variation in the direction of the grooves in the papillæ of the same row, and considerably more in some rows than in others; but the constancy in some of them is noticeable. In the larger papillæ the grooves are much more pronounced than in the smaller ones, in many of these latter the excavation being a pit rather than a groove. In the lower-jaw series of this species, the grooves of the inner rows extend crosswise to the axis of the head, and those of the outer row lengthwise, thus corresponding to the condition found by Solger in Gobius minutus.

In addition to the four series thus described, there are numbers of papillæ scattered on other portions of the head, particularly about the tip of the snout and on the opercular apparatus; in these regions they are particularly numerous on the suboperculum. Also on each side of the body, beginning immediately behind the pectoral fins, there are about thirteen transverse series, containing from five to ten papillæ

each; and still lower down are from five to seven additional transverse series, extending well down on the ventral surface of the body. It is possible that these lateral series are derived from a segmentally arranged type; but if to they have certainly deviated greatly from the typical arrangement, as they also vary both in the number of series and in the number of papillæ in each series. The papillæ here are considerably smaller, on the whole, than those of the head. There are, finally, a number of papillæ scattered around the bases of the fins, both pectoral and pelvic.

In Clevelandia there are about twenty-five transverse series on the sides of the body very uniformly segmentally arranged, being situated on the inter-myotomic septa. The series contain an average of about five papillæ each, though the number varies considerably. I have worked out the precise arrangement of the series on the septa, — for not quite all the septa have papillæ, — and of the number of papillæ to each series in a considerable number of specimens, as it has appeared to me that this may have considerable morphological significance. It is not necessary for my present purpose, however, to give the results in detail. It is worthy of mention that the transverse series on the body of Clevelandia are situated in shallow ditches, the anterior wall of these being deeper and more abrupt than the posterior. In no case have I been able to find the papillæ situated in canals, or in grooves that approach canals, as is so common in fishes, and is said to be the case in Gobius niger, by Merkel ('80, p. 28). All writers agree, however, that in the genus Gobius by far the greater portion of the papillæ are free on the surface of the body (F. E. Schultze, '76; Merkel, '80; Solger, '80). We know from the last two of these authors that both the genera Gobius and Gobiodon have free transverse series of papillæ on the sides of the body. With reference to this subject, Solger ('80, p. 378) says: "Bei Gobius konnte ich 'Querreihen von 3–7 Organen' constatiren; auf Beziehung der Organreihen zur Metamerie des Leibes achtete ich damals leider noch nicht. Auch Gobiodon hat am Rumpfe freie Seitenorgane, die in Querreihen auf Coriumpapillen stehen und höchst wahrscheinlich durchweg segmental angeordnet sind." And Merkel ('80) shows three of these series in his Figure 4, Taf. IV.

It being, then, evident that so many of the near relatives of Typhlogobius are provided with sense papillæ on the sides of the body, the question at once arises whether any are found in the corresponding region on the blind fish. Very naturally it was to the smallest specimens in my possession that I turned to begin the search for them. On

each of the two individuals 19 mm. long, papillæ were found on the sides of the body, and on one of them a few on the head, besides in the regions where they occur regularly In one of these the papillæ on the right side of the body were distributed in what I regard as representatives of nine of the transverse series described in Clevelandia. The first and second series behind the pectorals were represented by one papilla each; the third and fourth, by three papillæ each; the fifth, sixth, and seventh, by two each; and the eighth and ninth, by one each. The series were evidently segmentally arranged, though not all were on consecutive segments; thus between the third and fourth series were two myotomic plates; between the fourth and fifth, four plates; between the fifth and sixth, two plates; between the sixth and seventh, one plate; and between the eighth and ninth, two plates.

Figure 25, Plate IV., shows the arrangement of a group of papillæ on the right side of the head of this same individual. As seen by the figure, seven of these papillæ were much larger than the remaining ones, and were situated on quite prominent ridges of the skin.

Although the papillæ have been diligently searched for on the sides of the body of other specimens, they have been found on the two small ones only. The question at once arises, Are the papillæ absent from the larger ones because they have degenerated and completely disappeared during the life of the individual? All the evidence I have on this point is contained in the facts presented. That the papillæ have been found only on the two small specimens examined, and that they have not been found on any of the numerous large ones, certainly suggests very strongly an affirmative answer to the question. It must be said, however, that a considerable percentage of my larger specimens are not so well preserved but that the papillæ may possibly have been present in them and escaped detection. But some of them are well preserved, and were the papillæ present they would, I am sure, have been found.

That the sense papillæ are less numerous on Typhlogobius than on several, at least, of its near allies, is evident. The question may now be asked, Is it not possible that, although there has been no compensation for the loss of sight by an increase in number of the tactile papillæ, such a compensation has been brought about by a higher development of the individual papillæ themselves? So far as structural evidence is concerned, this is certainly far from probable. Figures 23 and 24 (Plate IV.) show sections of two papillæ of the inner mandibular series of Typhlogobius; and for the purpose of comparison a section of a

papilla from the same region in Lepidogobius is given in Figure 26. Between Figures 24 and 26 there is considerably less difference than may often be seen between sections of different papillæ of the same animal. Thus the sense cells proper (*cl. sns.*), which are very regular in their arrangement in Figure 26, are quite irregular in Figure 24; but Figure 23 agrees much more closely in this particular with Figure 26 than with Figure 24. Indeed, the difference is due to the position and direction of the section, both arrangements being found on sections of one and the same papilla at times. The cuticular spikes, so distinctly seen on the sense cells in Figure 23, are much less distinct in any of the Lepidogobius sections examined; but they are only exceptionally seen with such clearness in sections of the blind fish papillæ. It will be noticed that a considerable space (*tt.*) exists in Figure 26 between the sensory cells and the underlying nuclei of the supporting cells, in which there are no nuclei; and that such a space does not appear, at least conspicuously, in either of the figures from Typhlogobius. This, however, is not a difference of material significance, since in many sections of the papillæ of the blind fish such spaces do exist. In Figure 24, it will be observed that a blood-vessel, *va. sng.* (the leader from which has been misplaced in the engraving), penetrates far into the interior of the papilla. A similar vessel is present in Figure 26, though it does not extend quite so far into the base of the papilla, nor have I in any case found it to do so in this species, though it is true I have not examined as large a number of sections of Lepidogobius as of the blind fish; but the difference, if distinctive of the two forms, is nevertheless insignificant. Neither as regards the mantle cells (*cl. mt.*), nor the relation of the papilla to the epidermis, — i. e. its extending entirely through the thickness of it, — nor the way in which the nerve approaches and enters the papilla, nor the character of the immediately underlying sub-epidermal tissue, is there the slightest characteristic difference to be made out between the two species in such papillæ as are represented in Figures 24 and 26.

In only one point a difference may possibly exist between them, though I have not yet been able fully to satisfy myself of this. By Figure 23 it will be seen that the papilla is wholly and deeply buried in the epidermis, only a small pore (*po.*) communicating with the outer world. The apparent bridge across the pore near the papilla is probably a point of contact merely, as adjacent sections show. The whole appearance is as though the papilla had been withdrawn into the epidermis; for not only is the latter much thickened immediately around

the papilla, but the inverted hopper-shaped outline which the inner surface of the epidermis shows immediately under the papilla in most cases where the latter reaches out freely to the surface (as in Figures 24 and 26), is here entirely obliterated. Another fact that seems to favor the view that the papilla has been withdrawn, is the very distinct flask-shaped excavation in the summit of the papilla itself, seen in Figure 23 (*fos.*), while in the sections represented in the other two figures no such excavations are present. A natural explanation for this would seem to be that, on being drawn in, the middle portion of the papilla with the sense cells had been more depressed than the mantel cells. This may be the true explanation, but in one instance I have found the excavation in the papilla, even though the papilla itself protrudes through the epidermis, even more distinctly than in Figures 24 and 26 ; yet it should be mentioned that in this exceptional instance the papilla is considerably narrower in proportion to its length than those shown in the figures just referred to, or than they usually are. I have searched in vain for muscle fibres that could bring about such a withdrawal, and have no other evidence than that presented that it takes place ; nor have I often found the papillæ thus buried, and never in Lepidogobius. Leydig ('79, p. 25) has suggested the probability of the contractility of the cellular elements of the papillæ as the cause of an apparently similar condition in Acerina cernua.

A word should perhaps be spoken at this point on the possibility of the loss of sight being compensated by a higher development of the organs of hearing or smell. This subject lies outside of the purpose of the present paper, and I have given only superficial attention to it. The ears examined in dissected specimens mounted in glycerine do not appear unusually large. The minute structure I have not examined ; but from this morphological evidence, taken with the fact that all my efforts to get from my single living specimen responses to sounds of various kinds were unavailing, I am inclined to believe that the sense of hearing is not largely developed.

My sections of the snout show the olfactory epithelium to be very well developed, though apparently not more so than in other bony fishes, and certainly not so highly as in some of the long-tailed amphibia that I have examined.

What we know about the compensatory development of the tactile organs in other vertebrates with rudimentary eyes may be summed up as follows. It is well known from the writings of Tellkampf, Wyman, Leydig, Putnam, Wright, and others, that the tactile papillæ are well

developed on the head and sides of the body of both Amblyopsis and Typhlichthys. According to Packard ('86, p. 127), Tellkampf regarded these papillæ "as without doubt increasing the tactile sense." I have not seen this paper of Tellkampf's, and do not know whether his meaning would be that the tactile sense is increased as compared with what it was in the same species before it was deprived of sight, or merely that it is great as compared with other bony fishes. Leydig also believes that the tactile organs perform such a compensatory office ('83; see also Wright, '84, p. 272). Packard ('86, pp. 127, 128) gives extracts from several letters of Dr. John Sloan that are interesting in this connection. Although the writer does not expressly state his belief that the sense of touch has been highly developed for the purpose of compensating the lack of sight, he still gives very convincing evidence of its extreme acuteness from personal observation on the fishes in their native surroundings. It should also be noticed that he specially tested their powers of hearing and the effect of light upon them, and to both he says they "manifested total indifference." Sloan's observations were on Amblyopsis. Wyman ('72, p. 19) has described the ear of this species as being "largely developed" in all its parts, and Cope ('72, p. 410) found the sense of hearing "evidently very acute." As to the question whether the sense papillæ in Amblyopsis and Typhlichthys are in reality developed as a compensation for the loss of sight, the testimony furnished by Chologaster is of the greatest importance. Although this genus was discovered and named by L. Agassiz in 1843, its characters were best made known by Putnam. He ('72, pp. 22, 23) says: "In the genus Chologaster we have all the family characters as well expressed as in the blind species, though it differs from Amblyopsis and Typhlichthys by the presence of eyes, and the absence of papillary ridges on the head and body, and by the longer intestine and double the number of pyloric appendages, as well as by the position of the ovary."

In 1881, S. A. Forbes ('82, p. 3) discovered a fish in Southern Illinois which he identified as belonging to the genus Chologaster, but representing a new species. With reference to the point that we are now considering, the author writes: "The most important and interesting peculiarity of this species indicates a more advanced stage of adaptation to a subterranean life than that of its congeners. On all the surfaces of the head appear short rows of peculiar tubercles. . . . When thus exposed [by being freed from the adjacent epidermis], they closely resemble the papillæ of Amblyopsis in form and size, and are similarly cupped at the tip." Again (p. 5) he says: "The extraor-

dinary development, in only a part of the genus, of a special sensory apparatus peculiarly useful to a fish unable, for any cause, to see, points the same way, [i. e. to the supposition that this genus has a shorter subterranean history than Amblyopsis,] and gives evidence of a *progressing* adaptation of these fishes to their unusual abode. The intermediate relation of the sensory tubercles of Chologaster to the much smaller ones of young fishes and the permanent papillæ of Amblyopsis, points out the evident origin of the last through the permanency and higher evolution of structures evanescent in the young." This is probably the clearest case furnished by vertebrates of the loss of sight being recompensed by a higher development of the tactile sense.

As regards the tactile papillæ in the Cuban blind fish (Lucifuga), Putnam ('72, p. 9), who examined a specimen sent to the Museum of Comparative Zoölogy by the discoverer of the fish, Professor Poey, says: "In the Cuban blind fish we find ciliary appendages on the head and body quite distinctly developed, evidently of the same character as those of Amblyopsis, and answering the purpose of tactile organs. . . . There are eight of these on the top of the head, . . . and quite a number arranged in three rows on each side of the body, showing that the tactile sense is well developed in these fish."

This, so far as I am aware, is all that is known on the subject, and can be regarded as furnishing nothing more than a probability that touch papillæ have been here developed to compensate the fish for sightless eyes. The writer just quoted remarks further, that it is singular that the barbels on the jaws, so commonly found in the Cod family and its allies (to the latter of which the Cuban fish belongs), are entirely wanting. As is well known, Lucifuga is a cave dweller, and consequently the conditions which have produced its rudimentary eyes are more similar to those that have produced the corresponding change in Amblyopsis than to those that have had the same effect on Typhlogobius. And this fact may strengthen the probability above referred to; for, from the difference in conditions of life, Amblyopsis and Lucifuga are in all probability much more active than Typhlogobius, and this would make the tactile sense more useful to the first two species than to the last one.

We will now notice the condition of the blind deep-sea fishes with reference to the touch papillæ. The three forms described by Günther ('80), Typhlonus nasus, Aphyonus gelatinosus (p. 548), and Ipnops murrayi (p. 585), are all without barbels, and, so far as known, other special tactile structures. The two genera first named

belong to the same family as Lucifuga, and consequently the remarks made concerning the absence of barbels in the latter will apply in a measure to these genera, and with reference to Lucifuga receives more force by the statement of Günther that they "are Brotula organized for a subterranean life" (p. 547); and in the genus Brotula, which has eyes, the snout is provided with barbels.

Through the kindness of Mr. C. H. Townsend, naturalist of the United States Fish Commission Steamer "Albatross," I have been able to examine, though somewhat superficially, a specimen of Ipnops, — probably the same species as the one above mentioned, — and, so far as I could discover, Günther's statement that it is "deprived of organs of sight and touch" ('87, p. 190) is strictly correct. The same author makes the following as a general statement on this subject: "Special organs of touch are not more generally developed in deep-sea fishes than in the littoral fauna. . . . As such may be considered . . . the more or less detached rays of the pectoral fin of . . ., and especially of Bathypterois, which possesses but rudimentary eyes." ('87, p. xxxi.) And in another connection the same author (p. 722) says: "Beyond that depth [two hundred fathoms] small-eyed as well as large-eyed fishes occur; the former having the want of vision compensated by tentacular organs of touch, whilst the latter have no such accessory organs."

I have not been able to find any direct statements concerning tactile papillæ on the several species of blind Silurids of South America mentioned by Günther (Packard, '86, p. 107), nor have we any knowledge that such structures are found on Gronias, the blind representative of the same family from Pennsylvania.

The Integument.

I was led to a study of the integument by the question having arisen as to why the quantity of pigment should have *diminished* in it, while under the same conditions of life it had *increased* in the eyes. That such diminution had taken place in the skin was inferred from the generally much lighter appearance of the largest preserved specimens as compared with the smallest. In the latter, the whole dorsal portion of the body and head is covered with a great number of distinct pigment cells (Fig. 1), while the large specimens never present anything like so conspicuous a pigmentation; and in the majority of cases they appear, on cursory observation, to be almost white.

Closer examination shows, however, that the pigment is in reality

present in large specimens as well as in small ones, in quantity almost, if not quite, as great in the one case as in the other; but that it becomes disguised in the former case, and in a manner that will appear presently.

Figures 9 and 10, Plate II., are from sections of the integument and immediately underlying tissues of the dorsum of the head of two individuals, 19 mm. and 72 mm. long respectively. It will be noticed that the epidermis does not differ essentially in thickness or structure. In Figure 9 it is about 0.028 mm., while in Figure 10 it is slightly thinner, though in reality it should be a little thicker, some shrinkage having taken place here. With the sub-epidermal connective tissue (*con't. tis.*), however, the case is quite different. In Figure 9 its thickness is 0.056 mm., while in Figure 10 it is about 0.025 mm., over the pigment; and it will be seen that in both the pigment (*pig.*) is situated in the deepest stratum of the connective tissue, adjacent, or very nearly so, to the muscles (*mu.*).

Within the sub-epidermal layer, in all the larger specimens, there is found a dense and intricate network of blood-vessels and capillaries. In general, the vessels of this network appear to run quite uniformly in one plane, situated about midway between the epidermis and the pigment layer. In many places, however, they will be seen, in sections, to approach very close to the epidermis, or at least to its basement membrane, which is at times quite distinct. These vessels are shown in Figure 10 (*va. sng.*); also in Figures 4 and 11 as surface views from nitric acid glycerine preparations. Their walls are so thin as to be scarcely distinguishable from the surrounding connective tissue. Indeed, in parts of many sections their presence can be detected only by the blood-corpuscles, which are very different in appearance from the connective-tissue cells, owing to their larger size, more elliptical outline, distincter nuclei, and slightly yellowish homogeneous non-stainable (in hæmatoxyline at least) cell protoplasm. The connective-tissue layer in which these vessels are situated is somewhat different from either the layer above or that below it: its fibres are more closely compacted together, it contains more cellular elements, and it takes stain rather more readily than do the adjacent layers. I am inclined to believe that many of these cellular elements are leucocytes. I may here add that the blood-vessels shown in Figures 4 and 11 are none of them of capillary fineness, since in none of them are the blood corpuscles arranged in a single row, as is characteristic in capillaries. The capillaries are still smaller, and from the method of preparation and delineation are not shown here.

It is unquestionably to the presence of this highly developed vascular network that the pink color of the living fishes is due; and it is undoubtedly by this, in part, but mostly by the much thickened sub-epithelial connective tissue, that the pigment is disguised in the preserved specimens.[1]

And now as to the reason for this highly vascular condition of the skin, which is certainly unusual, as I have convinced myself by examining the integument of several other bony fishes, both by sections and by the same methods of treatment that were used in preparing the specimens shown in Figures 4 and 11.

I will consider the several explanations that have suggested themselves, in the order in which they have occurred to me.

When I first saw the living specimens, I supposed their pink color to be due to the fact that the pigment had disappeared from the skin on account of the constant darkness in which the fishes live; and that, it having thus become somewhat translucent, no scales whatever being present, whatever of vascularity there might be in the tissues of the body wall became visible through the integument. This explanation lost all its force, of course, as soon as it was noticed that the pigment is present in large as well as in small specimens, and that the blood-vessels are situated *between* the pigment layer and the epidermis, and not *under* the former. I would not be understood to mean by this that the pigment layer is so dense that it would much obscure the vascular-layer were it superficial to the latter.

The next hypothesis that presented itself to me was suggested by the fact mentioned by Dr. Eigenmann, that the crustacean with which the fishes so constantly live is also of the same pink color. Have we here a case of protective resemblance? An entirely satisfactory answer to this question cannot be given until we know more of the habits of the fish in its native conditions of life, and also of the structure and habits of the crustacean in company with which it lives. So far, however, as our present knowledge enables us to see, there are some quite serious obstacles in the way of this supposition. It is probable that the fish

[1] I may add, that on examining several large specimens preserved in alcohol exclusively, I find that the pigment is very distinctly seen on the whole dorsal surface, without removing the skin. As the epidermis in these specimens is quite loose as compared with that of specimens preserved in picro-nitric, picro-sulphuric, or Perenyi's fluid, I explain the greater distinctness of the pigment by supposing that in the alcoholic specimens the sub-epithelial connective tissue has shrunken more by dehydration than it has in the other methods of fixation, and also more than has the epidermis.

has adopted its present mode of life as a means of escape from its enemies, so that protective coloration could be of no use, and consequently natural selection would have no power to establish the color.

It is true that there are recorded a few cases of animals that are apparently protectively colored, which at the same time depend upon concealment to escape their enemies; e. g. the caterpillar of the moth Mania typica (A. R. Wallace, '89). But these are certainly very exceptional; and if the law of natural selection is to be held as applying to them at all, we are compelled to assume that either the coloration must have been produced in some other way than through it, or that neither the color protection nor the concealment is adequate in itself to effect the degree of protection necessary for the preservation of the species. On this supposition, it is possible that natural selection has been operative in producing the color; but Dr. Eigenmann ('90, p. 68) tells us that Typhlogobius "never leaves its subterranean abode"; and the extent to which the eyes are reduced affords very strong proof in confirmation of this statement. Again, on physiological grounds, it would seem that had the color been produced for the mere purpose of the color alone, it would have been effected by a deposition of pigment, and not by such an enormous increase in the quantity of blood-vessels and blood; for certainly the former would have been more economical.

And this brings me to what I believe to be the true explanation of the condition. I believe it to be for the purpose of cutaneous respiration. Says Prof. N. Zuntz ('82, p. 114): "Wo auch immer das Blut mit der Atmosphäre oder mit gashaltigem Wasser in Contact kommt, muss, in derselben Weise wie in der Lunge, ein auf Ausgleich etwaiger Spannungsänderungen hinzielender Diffusionsstrom der Gase auftreten." The conditions for such a diffusion seem to be present here. That cutaneous respiration takes place as a normal process in many vertebrates, both terrestrial and aquatic, is generally admitted by physiologists.[1] For the present purpose I need only to consider in some detail what is known about the process in some of the aquatic forms.

Spallanzani (1803, pp. 71, 114) was the first to show that the frog by means of respiration through the skin continues to live for a long time in air after the extirpation of the lungs. W. F. Edwards ('24, pp. 41–62) confirmed Spallanzani's results, and added the observation that this

[1] For a discussion of this question, see the larger works on physiology, and particularly Milne-Edwards, '57, pp. 632–635, and Hermann, '82, pp. 114–117.

animal would continue to live in water as well as in air, particularly in flowing water at a low temperature.

Berg ('68) investigated the same subject, and, while confirming the results of his predecessors so far as the fact of cutaneous respiration is concerned, concluded that the quantity of carbonic acid gas exhaled is less than that found by Regnault and Reiset. Less attention appears to have been given to the subject of cutaneous respiration in fishes than to the same process in amphibians and mammals; though Spallanzani, and later Humboldt and Provençal ('11, p. 86), found it to occur in these animals to a slight extent.

Quineaud ('73, p. 1143) found that an eel of 530 grams' weight absorbs 0.58 c.c. of oxygen in an hour through the skin.

With this attempted explanation of the color of Typhlogobius the question at once arises, Is this color peculiar to this fish, or is it common to all others that live habitually excluded from the light as this one does? If all the other blind fishes have the same color, and from the same cause, viz. from the vascularity of the integument, then we should have to suppose the same explanation to apply to all; and this would diminish its probability, though of course it would not necessarily wholly invalidate it. In speaking of the color of blind fishes, Professor Putnam ('72, p. 8) gives a list of seven partially or wholly sightless genera of the family Siluridæ, found in various parts of South America, Africa, and Asia. Of their color he says: "All the other members of this family [Siluridæ] having rudimentary or covered eyes are also dark colored; while the blind fish of the Mammoth Cave and of the caves of Cuba are nearly colorless." Concerning the color of Gronias nigrilabris, already mentioned in other connections, Cope ('64, p. 232) says: "The color of the upper surfaces, tail, fins, barbels, and under jaw is black; sides varied with dirty yellow, abdomen and thorax yellowish white." And this author remarks in the same connection that the "dark pigment of the skin of this animal comes off upon the hands in handling it."

Concerning the color of the several species of the three blind, or nearly blind, groups of the Gobiidæ other than Typhlogobius, I gather the following from Günther ('61, pp. 133–138).

In the characterization of the group Amblyopina the eyes are spoken of as "very small, and more or less hidden." No mention is made in this connection of the color, though the name Amblyopus roseus (Cuv. and Val., XII. 164), as applied to the whole genus Amblyopus, is given in a foot-note. Of the eight species enumerated one is said to have "eyes

inconspicuous," color "greenish olive (in spirits)"; the color of another is "greenish," no mention of the eye; another is "rose-colored," no mention of the eye, nor statement as to whether this is the color in life or in spirits; a fourth is "brownish with darker spots, . . . eye small and indistinct"; another, "eyes invisible," no mention of color. Of the remaining three, no mention is made of either the eyes or the color, but for the name in one species *rubicundus* is given as a synonym. Of the genus Trypauchen two species are described, one of which is characterized as "reddish (during life), brownish (in spirits)," the other as "uniform rose-colored." No mention is here made of the condition of the eyes, and I know them to be rudimentary only by the list of blind fishes given by the same author (Packard, '86, p. 107).

In the characterization of the genus Trypauchenichthys the eyes are said to be "very small, scarcely visible," and the only species described is "rose-colored (Bl.)." Nothing is given to indicate that these fishes live particularly excluded from the light. The genus Amblyopus is said to be "confined to the coasts, estuaries, and fresh waters of the East Indies, extending northward to China and Japan; one species from the west coast of South America." The genus Trypauchen is from the "East Indian Seas" and the "fresh waters of Borneo," and Trypauchenichthys is from "rivers of Borneo."

We are not informed whether the several shades of red here mentioned are due to pigmentation; but from the facts that there *are* several shades, that in some of the species the color seems to persist in the alcoholic specimens, and that the fishes come in a category many of which — particularly of the related genus Eleotris, with eyes normally developed, inhabiting much the same regions — are of similar shades of color, it appears probable that such is the case.

Perhaps the most interest attaches to the color of the Mammoth Cave blind fishes and those of the caves of Cuba; for these are without any question completely deprived of the influence of light. Cope ('72, p. 410) speaks of Amblyopsis spelæus as swimming "in full sight like white aquatic ghosts"; in his original description of Typhlichthys subterraneus, Girard ('59, p. 63) gives its color as a "uniform dull yellowish white tint"; and both these species as well as the Lucifuga are referred to by Putnam as being "nearly colorless," as already mentioned. Also Jordan and Gilbert ('82) describe both Amblyopsis and Typhlichthys as "colorless," and in the same way Günther ('80, p. 618), who regards the two as belonging to the same genus, speaks of the body as colorless.

I have dwelt thus at length on this question of color in other blind fishes because Eigenmann ('90, p. 68) has said with reference to the color of Typhlogobius that "in its pink color and general appearance this fish much resembles the blind fishes inhabiting the caves of Southern Indiana." I suppose this to refer to Amblyopsis, as there is not to my knowledge any other blind fish known from the caves of this region. Whether Eigenmann's statement about the color of the Indiana fishes is to be taken as opposed to those quoted from other writers or not, the most significant fact for our purpose is that there is certainly no such degree of vascularity in the integument of Amblyopsis as is found in Typhlogobius. I have had opportunity to examine a well preserved alcoholic specimen of this species, obtained by Professor Mark from Professor Putnam. I prepared fragments of the skin in the same way that had been employed in studying that of Typhlogobius, and found the blood-vessels here to be even less abundant than in the integument of the Clevelandia and Lepidogobius that I have examined.

The most serious objection, I think, to the supposed respiratory function of the skin lies in the thickness and density of the epidermis, and the fact that the entire surface is thickly beset with the slime-secreting cells (see Figs. 9, 10, and 17). I do not believe, however, that the epidermis here would offer greater resistance to the interchange of gases than would that of the frog; certainly, as regards the integumentary glands and their products, the frog's skin can hardly be more favorably constructed for a respiratory function than that of the blind fish. When we remember the dense cuticular layer that covers the entire surface of such animals as the earth-worm, where all the respiration must be carried on through the body wall, this obstacle does not seem so great. Moreover, in Cobitis fossils, where intestinal respiration is well known to take place to a considerable extent, although it was long supposed that no epithelium was present in the region of the intestine, — in which from the richness of the blood-vessels the respiration is supposed to be carried on, — Lorent has shown not only that there is an epithelium present, but that it consists of two layers, a superficial layer of flat polyhedral cells, and beneath this a layer of stratified cylindrical epithelial cells, among which are scattered beaker cells (Wiedersheim, '86, p. 572).

Of course the ultimate test of my theory must be made by physiological experimentation, and I hope to be able to do this before long. I cannot suppose gill respiration to be to any great extent supplanted by integumentary respiration, since the gills appear to be normally developed. It is necessary, then, to suppose that the latter method supple-

ments the former; and this may have become necessary from the peculiar mode of life of the animals. It is quite certain that the water of the small holes under stones, in which they live, would contain less aerating oxygen than would that of the open sea; and consequently a greater absorbing surface would be essential in order to effect a normal aeration of the blood.

Summary.

The facts observed and the conclusions reached may be summed up as follows.

The Eyes.

1. In the smallest examples studied the eyes, though very small, are distinctly visible even in preserved specimens, — so distinctly that the lens is plainly seen. In the largest examples, on the other hand, they are so deeply buried in the tissue as to appear even in the living animals as mere black specks, while in preserved ones they are in many cases wholly invisible.

2. Neither in small nor in large specimens does the epidermis over the eye differ in thickness or structure from that of adjacent regions. In the large individuals the much greater thickness of the tissue here is brought about by an increase in the sub-epidermal connective tissue, the growth of which can be seen taking place in the embryonal connective-tissue cells that are found here.

3. As is the case with rudimentary organs generally, the eye is subject to great individual variation in size, form, and degree of differentiation.

4. The only parts of the normal teleostean eye no traces of which have been found are the argentea, the lamina suprachoroidea, the processus falciformis, the cones of the retina, the vitreous body proper, the lens capsule, and in one specimen the lens itself.

5. In the parts present the rudimentary condition of the organ is seen in the very slight development of the choroid, no cellular elements being present in this excepting in the chorio-capillaris, and here to a quite limited extent, the rest of that layer being composed exclusively of pigment; in the fact that the choroid gland is composed entirely of pigment; in the fact that the iris, though of fully the normal thickness, is almost entirely of pigment, there being on its outer surface in some specimens a small amount of cellular material, which probably represents the ligamentum annulare; in the great proportional thickness of the pigment layer of the retina and the entire absence in it of anything except-

ing pigment; in the incomplete differentiation of the layers of the retina, there being in some individuals scarcely more than a trace of the external reticular layer separating the two nuclear layers, and there being in no specimen studied a retina sufficiently developed to enable one to homologize with certainty the layers marked out; in the minute size of the optic nerve, and the fact that it is ensheathed in a thick layer of pigment for nearly its entire course through the retina; and, finally, in the small size of the motores oculi.

6. The surest evidences of actual degeneration are found, first, in the greatly augmented quantity of pigment in all the portions that are at all pigmented in the normal eye; and, secondly, in the presence of pigment in regions where none is found in the normal eye, as in the hyaloid membrane (Plate II. Fig. 12, *pig.''*).

No undoubted instances of degenaration through the breaking down and dissolution of the tissue without the formation of pigment, such as have been described particularly by Looss, have been found, though in a single specimen (the one in which no lens is present) a process of this nature may be taking place.

7. On comparing the eyes of all blind vertebrates that have been most carefully studied, we find that, in the several degrees of incompleteness of development represented by the different species, all may, in a general way, be said to be passing along the same degenerative road. There are apparently, however, a few interesting exceptions to this. The most marked of these exceptions is found in the entire lack of pigment in the eyes of the Myxinidæ, whereas in all other rudimentary eyes an increase of this substance over what exists in normal eyes is found.

8. The eyes of blind vertebrates furnish very little evidence on the question whether structures in undergoing actual degeneration in ontogeny follow the reverse order of their phylogeny. The little that may be regarded as bearing on this point is without much doubt of an affirmative character. This is found in the breaking down and resorption of the lens, — habitually in Proteus, and probably occasionally in Typhlogobius, — possibly in the excess of pigment in the iris and pigment layer of the retina, and particularly in its occasional presence in the hyaloid membrane of the Typhlogobius eye, while no evidence of actual degeneration in the retina appears in connection with these. The possible case of a degenerating retina in Typhlogobius is neglected in this consideration, since, as pointed out, the lens being absent in the same eye, it is immaterial whether it be considered or not.

The Integumentary Sense Papillæ.

1. These have been considered only so far as pertains to the question whether they have been developed to compensate the rudimentary condition of the eyes; and it is concluded that such is not the case.

2. The facts that lead to this conclusion are the presence in several closely related genera — four at least — of the tactile papillæ with the same distribution as those of Typhlogobius, and in addition to this, on parts of the body where they are not found at all in Typhlogobius, excepting in the smallest specimens; and that the papillæ that are present in Typhlogobius are not more highly developed than those of corresponding regions in related genera.

3. In comparing the several species of blind fishes with a view to determining under what conditions the tactile sense does become developed to compensate the loss of sight, it is concluded that, while the greater activity of the cave blind fishes might explain their more highly developed tactile papillæ, this cannot be affirmed as a general law, since other blind fishes (as some at least of the deep-sea forms and probably also the blind Silurids) are without tactile papillæ, while we have no reason to suppose them less active than the cave fishes. It is necessary to have more knowledge than is yet possessed of the mode of life of the various blind forms before this question can be fully answered.

The Integument.

1. This structure has been studied with reference to the pigment contained in it, and the pink color of the living fishes.

2. Very nearly if not fully as much pigment is present in the largest as in the smallest specimens, the lighter color of the former being due to the obscuration of the pigment by a thickening of the sub-epidermal tissue between the pigment and the epidermis.

3. The pink color of the living animals is due, in great part at least, to a highly abnormal development of blood-vessels in the sub-epidermal portion of the integument.

4. So far as it has been possible to determine, this vascularity of the skin is unique in this fish.

5. The most probable explanation found of this condition is that it is for the purpose of cutaneous respiration.

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EXPLANATION OF PLATES.

All the figures except 20 and 26 are drawn from Typhlogobius californiensis, Steind.

ABBREVIATIONS.

bac.	Rods of the retina.
bac. cla.	Knobbed or club-shaped rods.
chr.	Choroid.
chr.-cpl.	Chorio-capillaris.
cl., cl.', cl.''	Refractive cells of retina as they appear at different foci.
cl. con't.	Cells in connective tissue.
cl. gn.	Ganglion cells.
cl. gn.'	Ganglion cells showing processes.
cl. mt.	Mantle cells.
cl. sns.	Sense cells.
con't. tis.	Connective tissue.
cp. sng.	Blood corpuscle.
crn.	Cornea.
crt.	Cartilaginous portion of sclera.
drm.	Derma.
ec'drm.	Ectoderm.
ex.	Outermost portion of pigment layer of retina.
fbr. Mü.	Müller's fibres.
fos.	Flask-shaped pit in papilla.
ful.	Tangential fulcrum cells.
glb. pig.	Pigment nodules, clusters, balls, etc.
gl. chr.	Choroid gland.
gl. muc.	Mucus glands.
i.	Innermost ends of the processes of pigment layer of retina fused together.
ir.	Iris.
leu'cy.	Leucocytes in retina.
lig. ann.	Non-pigmented elements of the iris, ligamentum annulare.
lns.	Lens.
m.	Middle portion of the processes not fused together.
mb. li.n. ex.	Membrana limitans externa.
mu.	Muscle.
nl. ba.	Basal nuelci. (See p. 65.)
n. opt.	Optic nerve.
n. pap.	Nerve to papilla.
ob. ex.	External oblique muscle.
or. ser.	Ora serrata.
pap.	Papilla.
pig.	Pigment.
pig.'	Pigment behind cornea.
pig.''	Pigment in place of lens (Fig. 7) and (Fig. 12) hyaloid membrane (?).
pig.'''	Pigment surrounding optic nerve.
pig. rtn.	Pigment of retina.
po.	Pore in epidermis.
pr'c.	Processes of the pigmented layer of the retina.
rt.	Rectus muscles.
rtn.	Retina.
scl.	Sclera.
set. cl. sns.	Bristles of sense cells.
spa.	Spaces in the connective tissue over the eye.
spng-bl.	Spongioblasts.
st. bac. con.	Layer of rods and cones.
st. con't.	Stratum of formed connective tissue.
st. fbr. opt.	Optic fibre layer.
st. lac.	Stratum lacunosum.
st. nl. ex.	External nuclear layer.
st. nl. i.	Internal nuclear layer.
st. rtl. ex.	External reticular layer.
st. rtl. ex.'	Non-nucleated spaces in *st. rtn.'*, the beginning of external reticular layer.
st. rtl. i.	Neurospongium (inner molecular layer) = inner reticular layer (preferable).
st. rtn.'	Undifferentiated layer of retina.
tt.	Non-nucleated tract between sense cells and mantle cells.
va. sng.	Blood-vessels.

PLATE I.

Fig. 1. View of the dorsal side of the head of an individual 19 mm. long, showing the distribution of the pigment cells, the folds of the skin, and the eyes. × 18.

" 2. Similar view of an individual about 55 mm. long. × 2½.

" 3. An individual of the same size seen from the ventro-lateral side. × 2.

" 4. Nitric-acid glycerine preparation of integument from the dorsum of the head of a specimen 72 mm. long, showing the blood-vessels and the pigment cells. — Surface view. × 59.

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B. Meisel lith. Boston.

PLATE II.

Fig. 5. Meridional vertical section of an eye from a specimen about 50 mm. long. × 150. The fold in the pigment layer of the retina is indicated at *. (See text, p. 63.)

" 6. Meridional section of an eye without a lens. Specimen 63 mm. long. × 88.

" 7. The section, not quite meridional, is from the same eye from which Figure 6 is taken, and is given to show the pigment mass (*pig.″*) in the place of the lens. Consequently only the pigmented portion of the eye is drawn. × 115.

" 8. A dissected acetic-acid glycerine preparation to show the eye muscles and optic nerve. × 60.

" 9. Section of the integument from the dorsum of the head perpendicular to the surface, from an individual 19 mm. long. × 450.

" 10. Section similar to the one shown in the preceding figure, but from an individual 72 mm. long. × 450.

" 11. Preparation similar to the one shown in Figure 4 (Plate I.), but from the side of the body. × 63.

" 12. Section, not quite meridional, from an individual 60 mm. long. × 115.

" 13. The pigmented portion of the retina and choroid, from the same eye. × 230. The fold in the pigment layer of the retina is indicated at *. (See text, p. 63.)

" 14. A small portion of the pigment layer of the retina, and the choroid gland with the optic nerve passing through it. Specimen 63 mm. long. × 300.

" 15. A small portion of the retina, showing the optic nerve passing through it. Same eye as that shown in the preceding figure. × 300.

" 16. The iris and the adjacent parts; same eye as that shown in Figure 5. × 350.

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Fold here

Fold here

PLATE III.

Fig. 17. Meridional vertical section of the eye of a specimen 19 mm. long. $\times$ 230. *α*, connective-tissue strands (see text, pp. 57, 58); *β*, ciliary processes ? (see text, pp. 63, 64).

" 18. Small portion of the retina of the eye shown in Figures 5 and 16. $\times$ 980.

" 19. A small portion of a section of the retina near the ora serrata from the eye having no lens. $\times$ 700.

" 20. Section of the retina of *Clevelandia*.

" 21. A small portion of the retina of the eye shown in Figure 13. $\times$ 350.

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PLATE IV.

Fig. 22. Rods from the same eye as the preceding (Fig. 21); a', b', outer members; a'', b'', inner members; c, portion of outer member showing the more transparent round spots. × 720.

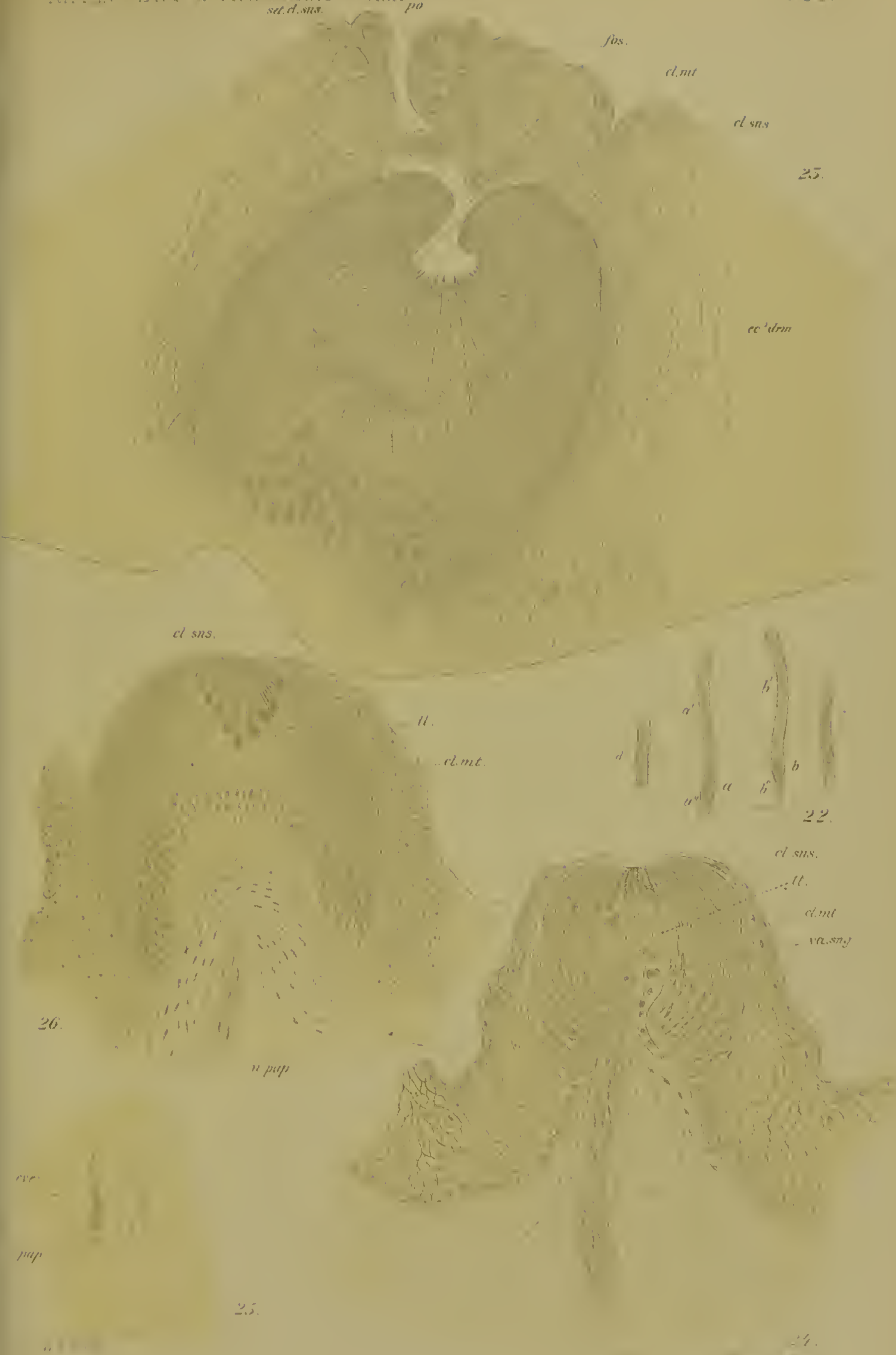
" 23. Section of a tactile papilla from the median lower-jaw series of a specimen about 50 mm. long. The section is not quite parallel to the long axis of the papilla, and this accounts for its appearing not to extend fully through to the deep surface of the epidermis. × 720.

" 24. Section of another papilla of the same series, same specimen as the preceding. × 350 about.

Note. — The leader from *va. sng.* has neither the right direction nor sufficient length to reach the blood-vessel in the axis of the papilla.

" 25. Diagram showing the arrangement and relative size of the papillæ found on the right side of the head of a specimen 19 mm. long.

" 26. Section of a papilla of the median lower-jaw series of *Lepidogobius.* × 340.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